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The nature and significance of
the various ends

Class A

Ends worthy for their own sake
& the realization of values

Belong to*

Ends to which we owe knowledge of
the constitution & relations of
the subjects & objects of these values

* Other ends belong to subordinate

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A. RUPERTI,
BOOK BINDER
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(For biographical sketch see page 84)

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Summary of
the topographical features and
evolution of the region
Sketch A.

The sketch gives the relationship of
different rock units in a typical area of
coastal Peru. The areas are grouped according
to the formation of the land by
geological and climatic factors.
The coastal plain is characterized by
sandy deposits and the mountains
are mainly composed of volcanic
rocks.

I.—Introduction.

"WHAT is the significance of *sex?*" is a special inquiry in the more general field of research included under the head of *Reproduction;* but nearly all the problems of the larger subject must be investigated if we wish to elucidate the more special one. The question presents both morphological and physiological aspects. Thus, we need to know the intimate structure of the sexual cells in the different plants and animals and the modifications this structure undergoes from the time the cells are generated until fertilization is effected. We can in this way compare the ovum and the spermatozoon and perhaps learn whether their functions are alike or different, and in what they differ. But we must also know how they compare with other cells, and are therefore at once compelled to treat the general subject of *Cytology.* This may conveniently be done in the following order: (1) Cell-structure in general. (2) The structure of sexual cells; the ovum (practically the germinal vesicle) and the spermatozoon. (3) The phenomena of karyokinesis. (4) The phenomena of fertilization.

Then in the next place it is necessary to make a comparative study of the methods of reproduction in the groups of living beings, following the phyla of evolution. In unicellular organisms we shall be mainly interested in the various ways in which reproduction is effected and the relation of these to the action of environing circumstances. Here we may see the origin of sex and henceforth trace its evolution. Then as we see how the multicellular individual arose from the unicellular one, and as we trace the evolution of more and more complex forms, differentiating into more and more numerous groups, the relations of the sexual method to other methods of reproduction will gain in interest and be best considered under the heads of *Alternation of Generations* and of *Parthenogenesis.* We shall also be specially interested in following the genesis of the sexual cells during the life-history of each individual, and so be involved in the mazes of *ovigenesis* and *spermatogenesis.* Incidentally *hermaphroditism* should be touched, and finally the morphological side of the question must conclude with a discussion of the significance of the *polar globules* and allied points.

Then on the physiological side, there is a vast and fruitful field both of accumulated facts and promising experiments for future research. The numerical relations of the sexes under fluctuating conditions so comprehensively discussed by Düsing in his memoir on the "Regulation of the Sexual Ratio," first invite our consideration. Next we cannot escape a discussion of the problem of *Heredity*, because this is the very soul and centre of all these other problems; and finally we must necessarily conclude by discussing the doctrine of the *Genesis of Species*.

We thus see that this inquiry is one of vast proportions, and can understand why it is still unsettled, in spite of the flood of speculations that all ages have poured upon it because of its absorbing interest and importance. But all except a very few of these attempts at a solution of the problem of sex are of no scientific and only of slight historic value. We shall only attempt a summary of our *present* knowledge of the subject as a *foundation* for future progress.

The stimulus this kind of research received through the labors of Darwin has not been effected in as great a degree among English-speaking savants as with the Germans. It is desirable that more interest in this subject be awakened among American naturalists, not alone for the sake of national pride, but also because the obscure recesses of this great problem can be illuminated only by the combined labors of many minds.

The earliest thinkers, acquainted only with the highest forms of life, naturally supposed that the interaction of the two sexes was necessary to produce a new being. Some, as Hippocrates and Galen, supposed that the two parents contributed equally and in a complementary manner to this achievement; others, as Aristotle, Fabricius, Harvey, thought that one parent was subordinate in his influence, being a mere stimulus to development. The discovery of the *ovum* and *spermatozoon* gave more definiteness to these theories, and so arose the schools of the *ovulists*, who saw in the spermatozoon a fertilizing element of the ovum, and the *spermatists*, who thought the ovum or the uterus to be a *nidus* where the *spermatozoon* was nourished and developed to the new being. Advancing knowledge dispelled the latter views and modified the former, but now arose the controversy of *evolution* vs. *epigenesis*, and so for a season attention was diverted from the main problem of the significance of sex.

Spontaneous generation once accounted for the presence of the swarms of minuter forms of life, but scientific study, aided by the microscope, showed that these lower forms of life multiplied by methods obtaining with the higher forms, and the doctrine of spontaneous generation was, by Tyndall's beautiful experiments, finally banished from the realm of the minutest infusorial life,—to which, as a last resort, it had been restricted. But, with the establishment of the law that all living beings are derived from pre-existing forms of life, we also learned that another method of reproduction, the asexual (agamogenesis), was more widely used by nature than the sexual one, and increases in importance as we descend the organic phyla,—is, in fact, the foundation on which the latter rests, and out of which it has been evolved as a rare and expensive, but useful, link in *generation.*

It is now a half-century since biology received its organon in the formulation of the *cell-doctrine.* From this doctrine we must start in every biologic inquiry. Stated briefly and in the light of the present, it stands thus: The body of any of the larger plants or animals is a mass of minute units, called *cells,* that are organized in a complex way into different orders of higher units, or parts, known as *tissues* and *organs.* The unity or *individuality* of the organism is secured by the harmonious working together of its organs, like the parts of a *mechanism,* towards simple results for the good of the whole. All living beings, compared as to structure (morphology), naturally fall into groups that are related like the branches of a tree (phylogenetic classification). At the roots we place the unicellular beings, then, as we reach the lowest and least subdivided branches, we find organisms represented by simple aggregations of cells like those which lower down live as independent beings; and, as we rise along the phyla, such aggregates become more and more complex in organization. In the development (ontogeny) of an individual its organization is established in the following manner. We start with a single cell, which produces an aggregation by continued self-division, and then the units differentiate into the tissues and organs, becoming successively more and more complex, so that the embryologic history—leaving out of consideration secondary or *cenogenetic* modifications—is a repetition of the stages seen as we ascend its phylum in the natural system. Such relations as these could have been established only by the actual evolution of living

beings along these lines, in the past history of the earth; and this is confirmed by the *palæontologic* record. We are thus convinced that organic beings are *genetically* related, and, therefore, the phenomena of reproduction and the question of sex must be considered in relation to the problem of the genesis of species.

The laws of organization of biologic beings find their analogues in civil and social organizations. Hence we often speak of the animal as the *cell-State*. As civilization progresses and *Society* is evolved, the unit, here the human mind, becomes more and more specialized in its activities, and the individual more and more dependent for his existence and welfare upon the fact that he is *part* of an organism,—the *State*,—which is complexly organized of many interworking and subordinate parts. How wonderful are the life manifestations of a State! and yet nothing is done except by the activities of the faculties present in each mind. The *division of labor* causes each function to be more efficiently exercised; but, what is more important, it is the *form* in which this is organized that impresses us and that makes the *individual*. In a similar way, a man may be said, philosophically speaking, to be only a developed amœba, even as a State is a man on a larger scale.

We are thus enabled to understand what is meant by the *Individual*. This term is purely relative, for in an organism where the subordinate units still retain a large measure of independence, the individuality of the lesser units detracts from that of the larger; indeed, the latter is not thoroughly established until the former is sacrificed, when the lesser units are so mutually dependent as to be mere *parts*. When this stage is reached the existence of the lesser units depends on the existence of the greater unit. Thus, when the organic relations or functions in a man's body are disturbed, not only does the man die (cease to exist) as an individual, but the cells also dissolve into the less highly organized substances of "non-living" matter. *Life* may then mean one or both of two things: 1, the activities of the organism (this is of course a mere summation of the activities of the cells); 2, the *form of organization* of these activities; this is a *relation*, an *abstraction*, but is necessary for the existence of life in the former sense,—*i.e., it makes the individual*. The controversies so often arising about these terms can only be due to a misunderstanding of the cell-doctrine.

There is, however, this difference between the *biologic* and the *social* individual,—the latter can be formed by *association* of units at first independent, while in the former *the cells are always genetically related.* The metazoa arose from the protozoa by a modification in the mode of reproduction by self-division, which caused the daughter-cells to remain united. Now, let all the other phenomena and forces remain as before, these daughters will soon divide again, they will not separate but will go on for a considerable period until an aggregate of cells results, then by the operation of the principles that produce *alternation* of *generations* in separated forms and *polymorphism* in *colonies*, there will follow what we term the *differentiation of tissues*, and lo, a metazoon. In a similar way, *among the Metazoa a multisegmented form must have arisen from one unisegmented by modified budding or strobilation.* Natural selection will account for the preservation of forms, but the cause and origin of new forms lies in the above laws of *organization.* We are now prepared for the next step in this argument. As *self-division* is the only form of reproduction that could give rise to the Metazoa, we understand why this is the mode which alone operates during ontogeny. It is also the usual mode of reproduction among the Protozoa. Once in a while under hard conditions of nutrition, etc. (perhaps so only as to its origin—Weissmann), the protozoan individual, too feeble to fight the battle of life alone, fuses (*conjugation*)with a neighbor (sometimes more than one?), and thus reinvigorated goes on in its former way again. Possibly *conjugation* is only one, though the most useful, of several methods by which *rejuvenescence* can be effected; at any rate we can see that by "sexual reproduction" we do not mean a new mode of reproduction contrasted with the asexual mode, but simply *a particular mode of asexual reproduction preceded by a particular method of rejuvenescence* (conjugation, fertilization[1]). Now when the Metazoa were formed by the non-separation of cells produced by binary division, those cells that required rejuvenescence were set free that they might conjugate, and *this is the origin of the ova and spermatozoa.* All the cells resulting from the repeated binary division of the fertilized egg are *homodynamous*, but all could not leave and be fertilized, because many were needed to differentiate into the various

[1] Van Beneden, Archives de Biologie, iv. p. 616.

tissues for the good of the whole. Even some of the generative cells had to serve their more fortunate brethren by giving origin to the accessory parts of the *generative tissues* that a few cells might be successfully prepared to perpetuate the species. All the tissues, including the *generative*, are based on a stroma of undifferentiated, "embryonic" cells, capable of dividing as they have in the past, and differentiating into their proper tissue when they have the chance, as in *regeneration* of lost parts. These cells are all the descendants of the original egg, and homodynamous with it and each other as if they were separate amœbæ. But after a certain number of divisions they lose the power of dividing further without fertilization and then they differentiate. Only the cells differentiated in the direction fitting them for fecundation ever get a chance to be fertilized.

Possibly this want of fertilization, more and more increasingly felt by the embryonic cells as they continue their final divisions, may explain *senescence;* but so long as we do not understand the nature of senescence in the Protozoa we cannot understand it in the Metazoa.

Growth is due in the Metazoa to the double process of cell-multiplication and cell-growth. May we not say that cell-growth is also partly a result of a reproductive process, and that the cell is a living unit by virtue of being organized? There can now no longer be a doubt of this. We can no longer speak of animals as "evolved from a homogeneous bit of jelly." Cells and the Protozoa and Protophyta in general, may be considered as illustrating as wide a diversity of differentiation and gradation of organization as we see exemplified in the larger units or in the social units (societies and states). We cannot conceive of life without organization. *The homogeneous cannot be called living.*

The cell-wall at first was thought of importance, but soon it was seen that this was a secreted product, and so its gelatinous contents, called *protoplasm*, next became the definition of a cell. But most cells had one or more "nuclei" in them, and this was conceived as a differentiated product of the protoplasm. Continued study of the *nucleus* raised its importance more and more, until at present some eminent cytologists are ready to make it the essential part, and the surrounding plasma almost as secondary as the cell-wall itself. Believing this to be the true view, we are ready to consider,—

II.—The Significance of the Cell-Nucleus to the Problem of Sex.

(*a*) CELL-STRUCTURE IN GENERAL.

Microscopic examination of cells in the living state, or treated by the simple *hardening*, *staining*, and *section-cutting* methods of a few years ago, can give us only a superficial knowledge of cell-structure. With such methods the first step taken was to distinguish the protoplasm as differentiated into the outer membrane or *cell-wall*, the more fluid and granular *contents*, and the generally spherical and central *nucleus*. The last body often carries a *nucleolus;* and nucleus and nucleolus may sometimes be increased in number, or, again, they may apparently dissolve to be later reconstituted. Our next step under this technique was to distinguish a primary and a secondary plasma,—the former the *protoplasm* proper, the latter the *deutoplasm* (paraplasm, metaplasm, etc.), formed by processes of *absorption*, *assimilation*, and *degradation* of the protoplasm. The former is active, *life-substance*, the latter passive, *food-substance*. The protoplasm is more firm and hyaline, abundant near the wall and the nucleus, and forms coarse trabeculæ, traversing and bathed by the deutoplasm. The latter substance is mainly "cell-sap," in which float *granules*, oil-drops, yolk-spheres, etc. The difference in the size of cells is due mainly to difference in the amount of deutoplasm they contain. We are not surprised, therefore, to learn that the yolk of a hen's egg is homologous with a microscopic cell, but we cannot say that it contains no more pure protoplasm than the latter.

The third step was taken as a result of studies of the phenomena of fertilization. The nucleus of the egg, the *germinal vesicle*, often shows a structure quite comparable to that of a "typical" cell, and the fact that it was seen to conjugate with the spermatozoon certainly pointed to its *autonomous* nature; but at first the true import of this conclusion was obscured by theories as to the multicellular nature of the ovum.

Our knowledge of the cell has, owing to improved technique, been wonderfully advanced during the last decade by the labors of cytologists, led by Strasburger and Flemming; and at present the work of Carnoy and of Gaule promises a new era in which the science of the cell shall rise to the dignity of a grand division of biology. We shall treat of *Cytology* only so far as a knowledge

of it prepares us to understand the import of *fertilization* as a morphological problem.

No one cell described in detail could be taken as "typical." It would be as absurd as to describe a horse as a typical animal. But the horse has tissues which are similar to those of widely different animals. So with protoplasm; it has a typical structure generally obtaining,—viz., *it is reticulated.* The *reticulum* is easily seen in "multipolar" nerve-cells, but almost any cell, when properly treated, will reveal it. (See Figs. 1–13.) A coarse reticulum has its trabeculæ themselves more finely reticulated. The reason for this structure is obvious. The thin threads of protoplasm are bathed by the cell-sap (the *enchylema*), and so the processes of *nutrition* and of *respiration* take place with rapidity. In the protoplasmic reticulum two elements are distinguished,—the clear *hyaloplasm*, which serves as a matrix for granular bodies of various sizes,—the *microsomata.* The microsomata are formed by the growth or the fusion of exceedingly minute grains, to which the term *granules* may be restricted. Then in the nucleus, when the microsomata grow or fuse to a few larger bodies, they readily come to be designated *nucleoli.* So these terms simply refer to size and not to definite substances, for one and the same substance occurs in all these forms, and there is every reason to believe that several different kinds of protoplasm occur in the form of these microsomata.

Another distinction is also made in that the protoplasm outside the nucleus is called *cytoplasm*, and that forming the nucleus is the *karyoplasm* (nucleoplasm). From this we get the terms cyto-hyaloplasm, cytomicrosomata, cyto-enchylema, or cytenchyma; and, correspondingly, karyo-hyaloplasm (karyaloplasm), karyosomata, karenchyma. Chemically, the *karyosomata* contain "*nuclein*," which is generally termed "*chromatin*" because of its great affinity for "stains." Gaule believes that he can differentiate two constituents of the karyosomata and two of the cytoplasm. He restricts the term chromatin to a substance having most affinity for *hæmatoxylin*, and gives the term *plasmosomata* to those nucleoli that especially fix *safranin.* The microsomata of the deutoplasm are said to especially stain by *eosin*, while *nigrosin* has a special affinity for ordinary protoplasm (cytaloplasm or cytosomata, he does not distinguish which). (See Figs. 49 *a–h.*)

It is pretty certain that protoplasmic movement is due to the al-

ternate contraction with thickening, and stretching of the fibres of the reticulum. The nodes of the reticulum come closer together in some one direction, and get farther apart in the direction at right angles to this; at the same time the microsomata at the nodes absorb the intervening microsomata. This looks as though the matter of the microsomata was subject to mutual attractions and repulsions, and then we could say that muscular movement is a special manifestation of those varied phenomena of division and fusion, attraction and separation of microsomata seen in karyokinesis.[1] However, this generalization cannot be made so long as we are uncertain whether the hyaloplasm or the microsomata are the primary thing, or whether they are independent but mutually reciprocal. If the microsomata (granules) are primary, then we must assume that the hyaloplasm is an aggregation of a special sort of these granules in a definite way to serve a definite function. From the optical properties of the hyaloplasm this structure must be regular and uniform. Others of these granules differentiate in various directions to serve various functions, and form, by various degrees of aggregation, the different sorts and sizes of microsomata. The primary granules from which all these other forms of protoplasm in the cell are derived must be endowed with the power of *growth*, of *reproduction* by simple division, and of differentiation or variation. They would be affected by stimuli and vibrations travelling in the hyaloplasm in which they live. They should be designated *gemmules*, because of all these properties. The *cell, on this hypothesis, is a gemmule state;* it is a complex organism, with parts structured and differentiated for special ends for the good of the whole. The membranes for protection and osmosis, the reticulum for movement and transmission of sensations, the gemmule for assimilation and reproduction. Degraded gemmules like differentiated and degraded cells form the various kinds of microsomata in the deutoplasm, and build up other parts of the cell. We shall see that the facts of cell-structure, of karyokinesis, and especially of fertilization, lend great weight in favor of this hypothesis. The *gemmules are the idioplasm.* They build up the cell in its peculiar characters and maintain it there. Under the above hypothesis the theory of Nägeli as to the structure of idioplasm will apply to the struc-

[1] See Figs. 12 and 93. *d*, and consult Van Beneden, Arch. Biol., iv. p. 343, and Melland, Quar. Jour. Mic. Sc., xxv., July, 1885.

ture of the gemmule, and not to the reticulum primarily as Nägeli intended. But the discussion of this point belongs under the subject of heredity.

It may be asked, what is gained by putting back the problems of life—of assimilation, of reproduction, and of heredity—one step; are they not as inscrutable as before? Undoubtedly they are, but we gain greatly by such a view as this. We can better understand the cell. Just as we simplified the problem of *life* as applied to the higher animals, by the cell-doctrine, so we simplify by as great a step this protean problem by means of the gemmule hypothesis. We must accurately determine what are the real labors of the gemmule out of which, by organization, the more wonderful phenomena of cell-life grow, and then we shall see that we have spanned by a large fraction the chasm between non-living matter and living matter. The albumen molecule is a very minute thing when compared with the gemmule, and there is plenty of room for one or two *stadia* of organization between, that would, when known, simplify the problem completely. On this hypothesis, also, cells must have a life-history in which they pass through stages of development and stop in various degrees of complexity as mature cells. The more highly organized cells must pass through the stages in which the less highly organized remain; and there is room here also for a *phylogeny* and for *cenogenetic* modification. Finally, the simplest cells we know, must be to some extent modified from the condition in which the original cell was. This must be taken into account in trying to derive "living" protoplasm from "non-living" matter. The first gemmule could arise only by organization of a lower order of life, and the first cell must have been an aggregate of like gemmules produced by binary division of a mother gemmule. Reproduction in this hypothetical first cell we may reasonably suppose to have been effected in two ways,—either by a division of the gemmule colony into two smaller colonies, or by a dissolution of its members when each gemmule was set free to become the progenitor of its own cell-state. When differentiation came in, the primitive mode of reproduction became modified, as follows: A few only of the gemmules were kept undifferentiated for purposes of reproduction. The others had to serve these, helping them to get better chance of food by carrying the colony about by amœboid or ciliary motion; others

to give protection; others, to furnish a special breeding-place for the gemmules differentiated into the nucleus; and so on. When the gemmule was set free, it more and more had to be protected by special envelopes, and so arose spores. When all the gemmules free for reproductive purposes went into the spores, the protoplasm remaining after the spores were set free could no longer grow, and hence live, and thus in reproduction by spores, as in gregarines, the mother-cell was left as a *corpse* when this sort of reproduction was exercised. (Fig. 27, *c*.)

But reproduction by binary division still continued, modified first as budding, where some of the reproductive gemmules were pinched off with a share of the cytoplasm. Here we must call attention to the fact that the *individuality of the cell does not depend on the number of idioplasm gemmules in it*, for all these, being undifferentiated, are, as it were, embryonic or *alike* and *mutually autonomous*.[1] They continually grow and divide, and two, resulting from one, do not produce a different kind of effect, but only more work than one. Indeed, the effect produced is not seen until they differentiate, and so present the characteristics of the cell. *This principle is extremely important for understanding the facts of fertilization.* It makes no difference whether the reproductive element set free contains *one or a million* gemmules, except that in the former case it *takes longer* to make as large a cell as the mother; in precisely the same way as it takes longer to raise a hydra from the unicellular egg than it does from the multicellular bud. The reproductive gemmules being now confined to the nucleus, binary division resulted in nuclear division; so far as it was advantageous that a large plasmodium-like cell should be produced, the new nuclei remained and nourished the common cell; and so far as the spreading of the cell over the habitat was of advantage, each daughter-nucleus took its half of the cytoplasm, thus producing cell division. This subject will be continued under the head of Karyokinesis. Continued binary division of the nucleus and the development of the products while the mother-cell remains undivided results in *free cell formation* (at least one variety of this). These cells often play the rôle of spores, and what is of importance when this is the case, the size of the spore is reduced in proportion to their number,—*i.e.*, to the number of divisions. In a number of the monads these spores are so

[1] Compare Nussbaum, Arch. f. Mic. Anat., xxvi.

minute as to be visible, only as a cloud of refringent points, under a magnifying power of four thousand diameters. (See *Roy. Micr. Journ.*, April, 1886.) Dallinger saw these points grow until they attained the size of nuclei, then there was differentiated a narrow zone, which increased in width around the nucleus and formed the cell. At the time this zone first appeared the hitherto homogeneous nucleus differentiated microsomata within it. (See Fig. 98, *a–c*.) As the flagellates seem to be the lowest of the forms of life in which all other groups converge, we should expect here the most primitive methods of reproduction. This mode of spore formation follows conjugation: the nucleus spreads by a sort of dissolution through the plasma as the case of the cyst forms. When the latter is broken, these spores imbedded in a plasma fill it. Have we not here a direct reduction to the gemmule condition, each gemmule being given a chance to start a new cell, *i.e.* a gemmule colony?

From the simple modes indicated above, we can easily derive the methods of reproduction obtaining among the Protozoa. If the whole or a part of the nucleus segments into spores which remain in a "brood pouch" in the cell-body, and are liberated as motile young, we get the "*germ balls*" of Stein. Compare Figs. 22, *d*, 23, 29, 30, 32, 33, 34. The structures here indicated are similar, but in many cases these nucleated bodies simply represent a stage of development or of kinesis of the nucleus, and are not liberated as spores. Bütschli is inclined to disbelieve in this mode of reproduction, but it hardly seems as if his objections sufficiently disprove the evidence we have of its existence.

If the chromatin, instead of remaining uniformly distributed in the nucleus, gathers into a particular body, which sustains the relation of a nucleus to the old nucleus, we get a *nucleolus*. This is a structure very generally found, especially in highly developed cells. The nucleolus is to be conceived as the primary body and the nucleus as secondary. Before the nucleus can divide the nucleolus must divide; but here we may get multinucleolated nuclei by the multiplication of the latter, while the former remains undivided. The general law of cell-life seems to be to conserve in the centre of protoplasmic bodies a supply of undifferentiated or primary substance (the *idioplasm*), and to surround this by concentric structures that protect it, and serve as organs of relation to the external world. The external envelopes

are derived by differentiation of this inmost substance. This idioplasm is continually throwing off centrifugally these secondary substances, and the continued life of the cell depends on its integrity. Reproduction always means that a portion of this substance has been separated from the remainder, and so acts from a new centre. The secondary plasmas are *mechanisms* for effecting such separations, as well as organs for other purposes. *All the biological manifestations of cell-life are due to the activity of these organs.* All the idioplasm does is to *grow*, by the growth and continual division of its gemmules, and to *differentiate*, by *organizing* in various relations for the different organs, perhaps accompanied by the chemical degradation of the units. What the chemical processes are that take place in the idioplasm unit, by which it grows and reproduces, must be referred for discussion to the subject of *Heredity*. The above is not an explanation, but simply a statement of the facts of heredity, as we conceive them, in this connection.

The forces active in the gemmule are, of course, the primary cause, and the reason for and explanation of the activities of the secondary plasmas, which activities are, as was said above, the phenomena studied in biology.

We can understand, in this light, how we always have structures and processes that obtain in one stadium of organization repeated in the higher, compound, or derived stadia. For this reason the nucleus is, when far enough developed, reticulated like the cell, and the nucleolus itself often repeats the structure. (See Figs. 2–13.) In the same way as we get three concentric structures simultaneously existing (Figs. 9, 13–15, 19–22, 26, 32, 42, 44, 49, 50–64), we may have a quadruple condition (presenting one or more nucleoli in the nucleolus), seen in Figs. 13, 26, *f*, 27, 33, 51, 53, 56, 58, 64; and possibly Fig. 56 is evidence of a quintuple state. The central body is always capable of generating the whole cell by a differentiation of its chromatin (see Fig. 49), and the central body of this new cell has like powers, and so on indefinitely.

We often have the nucleus or the nucleolus dividing into parts that are of unequal value, thus giving *chief* and *accessory* nuclei or nucleoli, as the case may be. (See Figs. 44, 49, 51, etc.) In this case the chief body only retains the reproductive function, and can, by suitable stains, be differentiated from the accessory

bodies. In this way Carnoy and Gaule have shown that such stains as hæmatoxylin and carmine are not tests for chromatin in a restricted sense, but that we must use safranin and methyl green. It is indeed a remarkable property of the idioplasm that it has a special affinity for aniline dyes.

In connection with the segmentation of the chromatin comes up the question of individuality. Is a multinucleated cell a single cell? If we understand that the chromatin is composed of many small units, like the soldiers in an army, we see that it can divide into bodies of various sizes, and these bodies can fuse again, just as the different divisions of an army may combine for any operation and separate once more for other duties. Such phenomena of the multiplication of centres of chromatin activity are illustrated in Figs. 1, 24, 25, 31, 42, and 48, or by a colony of flagellates, of hydroids, or by a tree.

Are all the bodies we see, such as nucleoli and granules in a nucleus, the result of *binary* divisions or of simultaneous segmentation of a single nucleolus, or are they produced by a sort of general dissolution? Conversely, what are the laws by which the different orders of bodies from granules to nucleoli are built up? This question is to a large extent obscure as yet. The phenomena to be explained in this connection are illustrated by Figs. 14, 15, 19, 26, 50–63. Even nuclei fuse (as see Figs. 94 and 97, *c*, and the sexual nuclei).

In some low forms of cells and in higher cells degraded by parasitism, such as yeasts and moulds, the nucleus may never take on the form of a compact body, but be present in the protoplasm in a diffused or granular condition. (See Figs. 14 and 15.) In karyokinesis and in maturation or development of nuclei, there seem to be phases in which this condition is represented.

Finally, we consider those forms of nuclei and of nucleoli where the spherical or elliptical shape is departed from to a large extent. Such are the *filamentous nuclei*. These are usually moniliform, being due to incomplete segmentation and to growth in one direction. (See Figs. 7, 19, *d*, 20, *b*, *c*, 28, 30, *b*, 31, 41, and 42.) In the higher tissue-cells, the *chief nucleolus* is present in this form, often being exceedingly long, and wound about in a way so as to give a reticulated appearance to the chromatin. It has been termed the *knäuel* by the Germans, which term means a *tangle*, usually termed a "skein" in English works on karyokin-

esis. (See Figs. 13, 19, *b*, 43, 44, 45, 46, *a–d*, 47, etc.) In Figs. 13 and 47 we see the chromatin present in these filamentous nucleoli has been complexly arranged in a reticulum and in a spiral respectively. A cross-section of one of these filaments (mitom of Flemming) cannot be distinguished from a section of a spherical nucleolus of like structure.

[NOTE.—After the above article left my hands an important paper by Altmann ("Studien über die Zelle," Leipzig, 1886) came to my notice. By means of fuchsin staining, followed by a wash of picric acid, a new element, the "*granula*," is brought to notice in the cytenchyma. These *granules* have hitherto been included with the cytenchyma in the general term *deutoplasm*, but Altmann believes they should be elevated to the dignity of an element in the protoplasm. To them Altmann ascribes the function of initiating and sustaining the metabolic or vegetative activities of the cell, while the reticulum mediates the motile functions. Morphologically, they are seen to grow and to multiply by fission or budding, so that he has formulated the law "*omne granulum e granulo*." He conceives the nucleus and nucleoli to be aggregations of granules, as are also the chlorophyl-corpuscles. (Compare Schimper, *Botanische Zeitung*, 1880 and 1883.) All this falls into line with the gemmule hypothesis, but the function of these granules cannot be so primary as he believes, if we are to credit the evidence obtained from experiments on enucleating cells. (See Nussbaum, A. m. A., xxvi.) Nussbaum found that if he cut an *Opalina* to pieces, the pieces deprived of nuclei continued to manifest movement, but did not grow. On the other hand, those pieces that had nuclei regenerated their lost parts. It is worthy of note that if a new formation was once in process of development, this was completed, even though the piece was enucleated during the process. This can be understood if we suppose that gemmules destined to repair the tissues had already migrated from the nucleus, though, of course, we are not confined to this explanation.]

(*b*) STRUCTURE OF THE SEXUAL CELLS.

In speaking of the sexual cells without distinguishing the ovum from the spermatozoon, it is useful to use the word *gamete*, from which we readily coin another useful word, *gametogenesis*, as including *ovigenesis* and *spermatogenesis*. In the present section we are concerned only with the changes which the nucleus of the gamete suffers after its final division in gametogenesis.

It is well known that in the earliest stages of gametogenesis there is little, if any, distinction between male and female cells; that in many cases the cell boundaries are not distinct, but we have a homogeneous albumen containing scattered nuclei, recalling a *syncytium;* that these nuclei have sometimes been seen to multiply by budding or by direct division; that the nuclei, as they grow, lose their homogeneity, and differentiate a reticulum and nucleoli in their interior, and simultaneously a layer of proto-

plasm, thin at first, grows out as an envelope about them, much as in Dallinger's *monad*. (See *J. R. M. S.*, July, 1886, and Fig. 98.) When the cells are completed, they multiply by indirect division (karyokinesis), but not to a very great extent, if destined to become ova. In this case a period of growth, of storage of nutriment for the future embryo, ensues, and when this work is completed, the ovum shows its homodynamous nature with the spermatozoon by completing its delayed divisions by the formation of the *polar globules*. Why these divisions are thus delayed will be discussed in its proper place.

If the ovum has its special work to do, division of labor has also given the spermatozoon its special work. For the large and stationary ovum must be sought out and penetrated, and so the enveloping cytoplasm is built up into the proper locomotor organs, which gives the male cell its characteristic and varied forms. We see that the characters which distinguish the male from the female gamete, or *vice versa*, are purely secondary and acquired characters, and, in the absence of these, we would be unable to distinguish sex. We shall endeavor to show that *the chromatin is not sexed*, but probably differs in the two cells by an infinitesimal variation. *So far as our idea of sex implies the differentiation of* MALE *from* FEMALE, *the chromatin is not sexed, but so far as it implies* DESIRE FOR CONJUGATION *with other chromatin differing from it by a slight variation, and likewise filled with a longing for conjugation, it* (the chromatin) *is sexed, but to this idea of sex the thought of male and female is foreign. Male* and *female* are ideas that have arisen in contemplating the different secondary mechanisms that have been evolved for the purpose of effecting conjugation; and these characters are the result of the operation of the same principles that have differentiated a gland-cell from an epithelium-cell.

But, let us see how these secondary or sexual mechanisms differ, and how the nucleus is related to them. We first consider the changes that are suffered by the nucleus of

THE OVUM.

Most of the observations on the *germinal vesicle* (nucleus of the ovum) relate to its behavior in relation to the polar globules, which does not now concern us; for we now know that this is simply the nucleus dividing by karyokinesis so as to become

sexually mature, and that, as in ordinary karyokinesis, the successive halves of the nucleus left in the yelk are the homologues of those extruded in the globules. We shall show that they are all *equivalents*, and there is not a separation of "male protoplasm" from "female protoplasm" in a once "hermaphrodite" cell.

When the few observations we have of the germinal vesicle during the period of growth are compared, we are struck by the apparent variety in the different cases. But this variety is probably due in part to a real variety in nature, and in part to the limited and partial knowledge we have acquired. From a comparison of Figs. 50–64, we may gather the following general features:

1. There is a richness of chromatin development resulting in great increase in size of the nucleus.

2. There is a considerable number of nucleoli developed.

3. A large portion of the chromatin is broken down and transformed into yelk. (See Fig. 50.)

4. The boundaries of the nucleus are often broken down or obscured; if not, they remain extremely distinct, enclosing a large cavity comparatively free from chromatin, and hence the name germinal *vesicle*. But with either change we find that one of the nucleoli has taken on functions that are probably nuclear in nature, and this has given countenance to the notion that the germinal vesicle may not be a nucleus, but is a cell. Such an assumption of the nuclear functions by a chief nucleolus is repeated over and over again in gland-cells, as in Fig. 49. We thus have a chief nucleolus or *germinal dot* and one or more paranucleoli. The latter simply break down, while the former furnishes the chromatin that divides in the polar globules, and at last conjugates with the male pronucleus; so that we always have a mass of the proto-substance conserved to carry on the existence of the gemmule colony, however much of the chromatin may be used for other purposes, and this reproductive substance is always conserved in the centre of the mechanism, surrounded and protected by at least two envelopes. If the nucleus buds, it produces *paranuclei*. Perhaps this is only a peculiar method of giving off nutritive substances to the cytoplasm. We must here observe that paranuclei, wherever found, are not necessarily homologous structures, either if more than one be found in the same cell or still less where we deal with phylogenetically

widely separated cells. When the germinal dot enters upon its activities as a nucleus it passes through the stages of differentiating a reticulum and nucleoli of different kinds in itself, as we shall see under *karyokinesis*.

THE SPERMATOZOON.

When the last division of the spermatocytes has taken place, the nucleus is practically ready for conjugation; hence, that its chromatin may meet the chromatin of the ovum, the secondary or *achromatic* structures of the nucleus transform themselves together with the cytoplasm (which seems to play a more passive part), into the suitable mechanism for effecting the transfer. In most cases the resulting form is filamentous, and has a spiral structure in some part. (See Figs. 66–93.) In such highly complex spermatozoa we may distinguish the following parts:

An outer *membrane*, which is perhaps the relic of the cell-membrane. A *head-cap*, posterior to which lies the *chromatin*. An *axial filament*, which may be taken as a sort of skeleton. (See Fig. 78, *c*.) Finally, there is a medullary sheath, best, sometimes only, developed in the "*neck*" or middle piece of the spermatozoon. This sheath is often composed of two or three bands that have been spirally twisted in opposite directions around the axial filament. Often one of the three is free and hung by a delicate mesentery, and thus may propel the spermatozoon like a screw. In the development of these parts, we first see the nucleus change its shape and become homogeneous, then the axial filament is seen stretching away from the nucleus and pushing the cytoplasm before it posteriorly as the nucleus does at the anterior end. The achromatic part of the nucleus is usually present as a paranucleus (see karyokinesis, Fig. 123, also Fig. 81), which in some cases is directly converted into the medullary sheath. Paranuclei (or granules) of a different sort are often present, and may have something to do in building the axial filament. All growth takes place in the neck just behind the head; and from this point the tail end is gradually pushed out as a completed structure. These accessory parts having accomplished their work of transferring the chromatin, which is to form the male pronucleus, are lost or dissolved in various ways. The chromatin is the essential substance, as we shall learn under "*Fertilization*."

The development of the spermatozoa in the special cases may be

learned by a study of the figures (Plate IV.) with the accompanying explanations. We could now pass on to the subject of fertilization did we not have connected with this phenomena another series of phenomena that can be understood only by reference to the facts of "cell division," to which we next direct our attention.

(*c*) KARYOKINESIS.

Two extreme types of cell-division are known; in one, the nucleus simply constricts into two halves that move apart, followed by a similar constriction of the cell-body, so that each of the daughter-cells is provided with its own nucleus; in the other type the nucleus undergoes changes by which it becomes invisible to the microscope, unless the cell be treated with proper reagents, and as the partition which divides the cell-body appears, there is gradually built up a nucleus in each of the daughter-cells. The former type is known as *direct division*, the latter as *indirect division*. The term *karyokinesis* (nuclear motion) is usually restricted to the latter kind of division, but we are learning that there are many forms of indirect division that gradually unite the two extremes, so that we can no longer make the above distinction. The term karyokinesis admits readily of a broad signification, and we shall use the word as including all sorts of nuclear transformations.

Our knowledge of cell-structure and of the nucleus has wonderfully increased since 1833, when *Robert Brown* discovered the nucleus while studying the generative organs of orchids, and *Von Mohl* (1835) first saw it divide. To-day we are making as rapid progress in this direction as ever, and there is no field of biological research which offers so great inducements to the investigator, or so valuable results as this.

In all our progress there has been but one tendency, and that is to show us that the cell, and especially the nucleus, is a complex and highly-organized structure. We can no longer use the term *protoplasm* in its old sense of *one definite substance* whose remarkable properties are due to the great chemical complexity of its molecule.

1. *Historical.*—In the works of *Schleiden and Schwann* (1838–1840), which established the cell-doctrine, the cell was described as originating by the activity of the *cytoblast* (the nucleus), which was itself due to a condensation of granules in the cell-substance

of the mother-cell. The endogenous origin of cells and cell-nuclei was, however, gradually overthrown, and in 1855 Remak established the generalization that all cells are due to the division of pre-existing cells in such manner that the nucleolus first divides, then the nucleus, and lastly the cell-body. This schema could rest only on the facts of direct division and a superficial observation of indirect division. As soon as the latter was carefully studied by *Hoffmeister*, in 1867, he found that the nucleus disappears and two centres of attraction arise in the cell, in connection with which the daughter-nuclei were built up. These facts had been observed in animal-cells already in 1858, by *Munk*, so that the view that a cell must return to a cytode condition to divide and so, in a manner, be rejuvenated, and produce new nuclei endogenously, was fairly established. This school was strengthened by receiving the support of all who had observed the maturation of the ovum (except Warneck, 1850), for here it was seen that the germinal vesicle disappears before segmentation, and that the nuclei of the segmentation products arise as new structures, and, moreover, *Valette St. George* had, in 1866, shown that the ovum is a cell, the germinal vesicle a nucleus, and the germinal dot a nucleolus.

The complex nature of cell-structure was surmised by *Brücke* as early as 1861, although the microscope had then only revealed granules, and that these were at times arranged in a radiate manner with reference to the nuclei.

In 1865, *Frommann*, through extended research, described the reticulate nature of protoplasm and generalized that this was the typical structure of protoplasm, but his views remained for many years unnoticed.

In 1873, *Heitzmann* advocated the view that whenever a protoplasmic mass was fully developed it became vacuolated, and so showed a reticulated structure in which the nodal points appeared as granules. The nucleus is only a large nodal point in the centre, and as this developed it repeated the process, and finally the nucleolus in a mature cell takes on the reticulate structure. He laid the basis for Nägeli's theory of heredity by advancing the notion that the reticuli of all the cells in the body are continuous, and so anticipated modern studies of protoplasmic continuity.

This year is memorable as marking the beginning of studies

on karyokinesis. The stimulus came from a paper by *Schneider*,[1] in which the different phases were pretty well described, though their connection and sequence were unknown. Even the spindle and cell plate were figured. *Bütschli* and *Fol* confirmed these results, the former mainly as to the nuclear rosette and its separation into two halves to constitute the daughter-nuclei, while the latter got the asters and spindle best; hence the former agreed with Schneider that there was no deconstitution of the nucleus, while the latter inclined to side with the orthodox school.

Auerbach now appeared with his "Organologische Studien" (1874). He starts with Heitzmann's views as to the organization of protoplasm, but considers the nucleus to be a sap-cavity into which molecules of protoplasm wander and grow to become nucleoli. These multiply by division, so that old cells have many nucleoli. The cells of highly-organized tissues, he says, have more nucleoli than cells lower in the scale of organization. The nucleoli are young cells, and they are simply separated into two groups in direct division; but in indirect division, which he distinguishes as *palingenetic*, these are dissolved into a molecular state in the nuclear sap, and then absorbed with the sap by the cell-plasma. This process is termed *karyolysis*, the spindle with its polar asters is the karyolytic figure and the simple expression of the streaming out of the nuclear substance. Later, near each star, the sap and molecules return to form a daughter-nucleus. This seemed a pretty fair explanation, and *Flemming* at this time was much influenced by it.

Bütschli, however (1875), opposed the theory, though he modified his former view of the simple persistence and division of the nucleus to the view that the nucleus is *reconstructed* into a spindle, at whose equator the fibres become thickened to form the nuclear plate, which plate by splitting passed its halves to the poles of the spindle to be re-formed into nuclei. In the same year the first edition of *Strasburger's* work on cell-division appeared. This treated in the main of the plant-cell, where the spindle thickenings after separating leave between themselves connecting fibrils that are more prominent than in the animal-cell. These he called *nuclear fibrils*, and at their equator a second set of thickenings appear that go to construct the dividing wall between the new cells, hence he named it the *cell-plate*. The

[1] A list of the papers referred to will be given at the close of the article.

second edition of this work appeared in 1876, and the third in 1880. In the last he changes the name he gave the connecting fibres to *cell-fibres*, because he supposed that they were formed from the cytoplasm penetrating into the nuclear matter at the time of the deconstitution of the latter.

Van Beneden, on the other hand, agreed with Bütschli that the spindle comes from the old nucleus. He distinguishes between the nuclear *sap* and the *nuclear essence*. The connecting fibrils are of the same essence as the nuclear disk, and are due to the drawing out of the elements as they segment into the daughter-disks.

In this year, also, *Hertwig* showed that the egg-nucleus does not disappear during cleavage, but passes through a metamorphosis similar to the cell-divisions described by Bütschli. At the poles of the spindle ~~and~~ in the centre of each aster he finds a *polar corpuscle*. Fol had seen corpuscles in the stars, but had confounded them with the daughter-nuclei. The following year, 1876, Fol corrects this error. *Balbiani* found the nuclear plate to be composed of *rod-like elements* that were composed of *granules*, but these views were unnoticed, so that *Pfitzner* received the honor of their discovery five years later.

At this time the elements which compose the nuclear plate were not distinguished from the spindle-fibres, due to the fact that reagents which made the one visible left the other obscure, hence there was a good deal of contradiction in the results, which was unreal.

In this year *Bütschli's* chief work appears. He supposes the infusorian nucleus to represent the original type of nucleus. He thinks the cytoplasm stimulates the nucleus to division, though it may not itself necessarily follow the example. The rays of the stars are not the expression of attractive forces of the nucleus, but are rather due to a chemical influence. He found that the asters when they first appear near the nucleus, are not necessarily at opposite poles. R. Hertwig had divided the nuclear matter, like Van Beneden, into sap and nuclear substance, *Strasburger* now proposes the following scheme. There are in the nucleus three formed substances, one of which is active. ~~By the excitation of~~ the cytoplasm the active substance gathers at the poles of the nucleus, leaving the spindle-fibres stretching between; the latter are cytoplasmic in origin, and the polar substance acts on them just as it acts on the fibres of the cytoplasm which form

the stars, hence the general disposition of the polarized molecules in rows radiating away from the polar area. The third substance is first repelled from the poles to form the nuclear equatorial plate; but in some way there is a change of polarity by which it is subsequently attracted to the poles, and so the plate splits in two (it might also do this through internal repulsion, but, as we shall show farther on, there is no necessity for a physical explanation). This is perhaps the best of the few theories which have been advanced to account for the phenomena.[1]

On the question of the solution of the nucleus, *Fol* now took a middle ground, holding with Strasburger that the cytoplasm entering formed the spindle, but the nuclear matter simply became continuous with the cytoplasm through the dissolution of the nuclear membrane.

In 1878, *Schleicher* advanced the view that the protoplasm was composed not of parts that had a fixed relation to one another, but of units that were independently mobile, and so all the structures were amœboid in form, hence there could be no definite phases during cell-division, wherefore he proposed the term *karyokinesis* to designate the phenomena. On the other hand, *Flemming* had, by careful staining, worked out the series of forms through which the nuclear matter passes during karyokinesis. He did not get the spindle well because, as he showed the next year, this was composed of non-stainable matter. The resting nucleus consists of a vesicle enclosing a reticulum and one or more nucleoli. This reticulum is changed to an exceedingly long and intricately wound filament, at the same time the nucleoli dissolve in the sap and the filament absorbs the material. This is the phase of the *close knäuel*. (Fig. 112, *a*.) The filament now shortens and grows thicker, passing through the open knäuel stage, until it shows as a *rosette* (Fig. 111, *e*), with loops turned peripherally and towards the centre. Then the outer limbs of the loops break, leaving a lot of V-shaped filaments having their apices towards a common centre. (Fig. 105, *f*.) This is the "mother-star." Meanwhile the central point of attraction splits and moves to the poles, where asters now appear. This is accompanied by alternate expansion and contraction of the

[1] We give the theory in its most developed form, third edition of Strasburger's work, 1880, where he slightly modified it from its original statement in the second edition.

nuclear star (diastole and systole), and finally results in its flattening into an "equatorial plate" (Fig. 113, *d*); then each loop splits lengthwise, though it may have done so while still in the mother-star (Fig. 119, *e*), and thus formed the "fine-rayed star." The halves of each loop become separated and grouped in a "dyaster," or two daughter-stars, passing through the phase which shows as a splitting of the equatorial plate. Then the apices of the loops (travelling along the spindle-fibres) are drawn towards the poles (Fig. 112, *e*), drawing the limbs after them, and so reach the pole. Here they form into a figure like the old mother-star (Figs. 112, *f*, 105, *h*), and return, by uniting ends through the rosette (Fig. 118, *f*) into the knäuel form, and finally become like the mother-nucleus.

The next year Flemming divided cell-division into *direct* and *indirect*. He limited the former to motile cells, and accepted Schleicher's term as applying to the indirect kind. He thinks the nucleoli are an accidental thing in a nucleus, and according as nuclear substance stains or not he calls it *chromatin* and *achromatin*. In the same year, 1879, Fol proposed his electrolytic theory of cell-division. He believed the nuclear reticulum was directly transformed into the spindle, and the nuclear plate was due to an equatorial thickening of its fibres.

Strasburger's studies gave him different results from Flemming. In plants the phases are not so marked, but may give a spindle figure of chromatic granules arranged in rows like the staves of a cask; and the daughter-nuclei arise through the simple breaking of these across the middle. (Figs. 115, *a–d*.)

In 1881, *Retzius* had confirmed the phases of Flemming, but showed that the rosette must be given up, as segmentation of the knäuel may take place while in the loose or open knäuel stage. (Fig. 112, *b*.) He says the chromatic substance is contained in a hyaline matrix, as Pfitzner has shown, and most of it is absorbed by a particular node or nodes, and these are the nucleoli.

Pfitzner, this year, called attention to the fact that the nuclear loops are composed of granules like a row of beads, and that the loop splits by the segmentation of each granule. He thought these granules to be the protoplasmic molecules, but later (1883) said they were independent and individual units in the nuclear structure. (See Fig. 114, *a*, *b*.)

In 1882, Strasburger proposed the terms *cytoplasm*, *microso-*

mata, *nucleoplasm*, etc., which we adopted in Section *a* of this paper. He studied more carefully the method of rearrangement of the loops in the equatorial plate during its division, and finds that it is more complex than Flemming made it, for the old bend straightens out, and one end of the loop gets drawn towards the pole, and then bends like a hook, and this new bend travels along the filament to its middle point, thus making the two limbs equal, while at the same time the loop is drawn polewards. Strasburger had not yet discovered the splitting of the loops, so that he had as yet only an imperfect notion of how the rearrangement took place. (See Figs. 118 and 119 for the actual facts.)

In this year appeared *Flemming's* systematic work on the cell, and in it he accepts the criticisms of Retzius and Strasburger, so far as they relate to the rosette phase and the "rearrangement." He doubts if there is a reticulum in cells, or at least in nuclei. The appearance may be due to the optical effect of a closely-wound filament or *mitom*, the sap is the paramitom, and karyokinesis should be termed mitokinesis, or mitosis. Besides the mitom there are chief and accessory nucleoli. He gives up the idea that the chromatin may dissolve in the cell-sap. He gives us the term *spirem* for the knäuel phase. Rearrangement in the equatorial plate is termed *metakinesis*. He uses the term aster for the star-form of the mother-nucleus, and dyaster for that of the daughter-nucleus.

In 1883, *Pfitzner* makes three sorts of chromatic substance in the nucleus. The substance of the spindle, hitherto called achromatic, he terms *parachromatin*, while the sap only is true achromatin. The nucleolus has *prochromatin*, while the mitom has the true chromatin. In the resting nucleus there may be, besides Strasburger's membrane, which belongs to the cytoplasm, a true nuclear membrane of parachromatin.

Roux, in this year, proposes a theory of karyokinesis, based on the idea that there is a mixture of qualities in the chromatin, etc., and that these have to be distributed in a definite way between the daughter-cells at each division. Hence the complicated machinery.

In 1884, *Rabl* seeks to show that there never is a simple filament in a cell, but that the loops pre-exist even in the resting state, and that in this latter state the chromatin flows out along definite paths into finer and finer branches, which never anasto-

mose, but may swell up at points, where a special lot of chromatin gathers, and there form nucleoli. The cell is heteropolar, always having the apices of the loops directed towards the principal pole. (See Fig. 113, *a–f*.)

Heuser agrees with Rabl in finding the mitom segmented in the resting phase.

In this year *Strasburger* discovers the splitting phase in certain plant-tissues. (Figs. 118, 119.)

Carnoy now comes to the front with important contributions. He finds, what has not been noticed by previous observers in its true light, that there exists a true reticulum in the nucleus, like the reticulum in the cytoplasm (Fig. 4), but that the mitom in its convolutions hides this, and gives us the aspect of a coarser reticulum (Fig. 3), which is the one referred to by previous investigators. The mitom may be itself reticulated (Fig. 13), or its segments be short and rod-like in some cells (Figs. 123, 124), but besides these there are the nucleoli. All the nucleoli are not composed of true chromatin. There are one or two that are composed of *plastin* (Figs. 44, 124, *b*, *c*), like the true reticulum, and with it and the membrane become transformed to the achromatic or spindle part of the figure. The phases of Flemming are realized only in a limited number of cases, and there appears to be the utmost variety in the karyokinetic figures; we may get forms where the nuclear reticulum does not become transformed, although the mitom may segment. (Figs. 109, 110, *stenotic division.*) Again, the achromatic part of the figure may in one and the same cell differ under different circumstances from great complexity to simplicity of structure.[1]

Platner has also made important contributions (see Fig. 123, *a–gx*); but these will be considered in another connection.[2]

Thus we get a notion of the cell as a most varied organism. Cells may be as varied among themselves as the higher organisms. But we have hardly begun to get an idea of the variety of

[1] See also, Lee, "Carnoy's Cell-Researches." Q. J. M. S., April, 1886.

[2] The latest paper by Platner (see Bibliography) has just come to my notice. Platner thinks the spindle fibres are one continuous filament in which is a protoplasmic streaming in one direction. Each meridian bears a karyosoma that splits, because the fibre splits; this, always in a meridional plane. The parachromatic mitom is so wound that the current is towards opposite poles in neighboring fibres after the splitting, hence the daughter karyosomata are swept to their proper poles. This theory appears to be as weak as its predecessors.

karyokinetic phenomena; what is to appear by future study we can only vaguely imagine. The phenomena of cell-division cannot be purely physical phenomena. They are living phenomena, and show they are subject to the laws of heredity and evolution of adaptation and variation. If this be so, we can understand karyokinesis only through comparative studies, just as we study the laws of variation and evolution, of homology and affinity with higher organisms. It becomes important, therefore, to understand karyokinetic phenomena among the Protozoa. Recent studies in this line have shown that here we may get nearly as complex figures of karyokinesis as in tissue-cells; but from this we get all grades down to the simplest direct division. We learn that nuclei may be alike in distantly-related forms, while closely-allied forms may have very diverse nuclei.

2. *Protozoa.*—These organisms present, as we should expect, a great variety of nuclear forms and karyokinesis. The differentiation has been in so many different directions, with the acquirement of secondary characters whose physiological significance we can hardly guess, that it is perhaps impossible to connect the forms. Frey thinks the vesicular form of nucleus is the primitive one, but most writers agree with R. Hertwig in deriving this form from a solid form through vacuolation of the latter, which leaves the chromatin either all in a cortical zone, or else in one or more nucleoli; and this process may be repeated in a nucleolus when this becomes large and important. Gruber suggests that in a primitive state the chromatin was present throughout the cell in a granular form, as in Trichosphærium, Pleurophrys, Trachelocercus, Chœnia, and others, and that solid nuclei arose by fusion of these granules, or by some of them remaining in close union following their multiplication. But it must be observed that this granular condition could easily arise by the segmentation of larger bodies and so be secondary in character. In some forms we get either many small nuclei or else granules, besides one or more chief nuclei, and, according to Altmann, this is true of all tissue-cells, so that we have nuclear bodies first differentiated in two directions, the granules serving some nutritive or other function, while the nuclei retained the office of being the primary reproductive bodies.

The next differentiation arising would be the differentiation of the nuclei into two kinds, which in some Ciliates have acquired

considerable independence and act quite differently during division. We know them as nuclei and nucleoli, or as nuclei and paranuclei, respectively. Better terms are Huxley's *endoplast* and *endoplastule*, as not implying homologies which are probably false. In massive nuclei the chromatin exists in a fine net-work, which gives the appearance of granules in the resting phase and of fibrillæ during division. In Gastrostyla the endoplastules divide by a true spindle and a nuclear plate of karyosomata. Nearly all the nuclei of Opalina are of this sort.

The substance of the nucleus may differentiate into two sorts that gather in two portions of the nucleus, either by polar differentiation or by centripetal differentiation. One substance is hyaline, the other granular; examples are Leptodiscus, Spirochona, and Noctiluca. In Spirochona it is the endoplast which has this structure, and it divides by a complex kinesis. A nucleolus appears in the clear part, which becomes transformed into fibrils while the hyaline portion gathers as two polar plates that separate, and so, as it were, tear the nucleus in two. The three endoplastules present divide by simple constriction at the same time; and here also there are polar plates of a substance different from the equatorial portion.

In a different direction we get the vesicular differentiation, and this is most common in the lower Protozoa, and is that from which the metazoan cell-nucleus is derived. In Rhizopods we may not only get many nuclei (about two hundred in Pelomyxa), but each nucleus may present a great variety of phenomena. There may be a central nucleolus, and this nucleolus may be composed of many microsomata, or the microsomata may separate as so many nucleoli, or again may fall into granules. Together with all these forms there may be a cortical shell of microsomata, for examples, see Figs. 14, *a*, *b*, 20, 22. The multinuclearity of many of the Protozoa is due to the fact that cell-division is purely facultative, and has not been inseparably associated with nuclear division. When it takes place, as in Opalina, ~~any~~ a variable number of nuclei may be separated away in the daughter-cell. In many cases the nuclear divisions affect only the chromatin, while the hyaloplasm and its nucleolemma remain as *funiculi* uniting the segments. (See Figs. 42, 31, 29, 28, 41, etc.) The microsomata of a nucleolus or of a karyosoma behave in the same way; as in Figs. 19, *d*, 43, 114, 115, 123, *g*, 124, *o*.

In Radiolaria we get a multitude of small "massive" nuclei that divide by amœboid constriction (Fig. 25), and in the central capsule vesicular nuclei, whose different metamorphoses are shown in Figs. 16, 17, 18, and 19.

In division of vesicular nuclei we get, as the simplest form, the Remakian scheme. (Fig. 100.) Next we may get the granular contents arranged in fibrils that are bisected by the constricting nucleus (Fig. 101), or they may remain in the granular state. (Fig. 99.) The most complex case is given by *Actinosphærium eichornii*. (Fig. 103, *a–q*.) Here the nucleolus separates into two bodies, one containing chromatin and one the parachromatin; then each body segments into fine granules; these granules get arranged in fibrils; the chromatin-granules fuse to karyosomata lying in an equatorial plate in the spindle formed by the parachromatin; the karyosomata divide into daughter-karyosomata that pass towards the poles; on its way each daughter-karyosoma segments to microsomata; the microsomata segment to granules, which, however, form separate karyosoma-like masses until they are absorbed by the polar plates. The latter are due to the fact that the external protoplasm had gathered at two opposite poles of the nucleus and had attracted the parachromatic cortical layer of the nucleus. Why the protoplasm should gather at the poles and so induce nuclear division is unknown. Possibly substances in the nucleus have first passed to the poles and attracted the cytoplasm. These substances may be the segments of the paranucleolus, for it is possible to derive the spindle-fibres from a differentiation of some of the chromatin-granules into hyaloplasm.

It is rare to find the nucleolus (or the granules that represent it when it is segmented) in the same condition during nuclear division as during the resting phase. There is a cycle of changes, so that one condition has to be assumed for division, and then the chromatin returns through inverse stages to its resting state. The phases of this cycle may be few or they may be many, and besides, the phase in which the nucleus rests may be in one case in one point of this cycle, in another it is a different phase of this cycle. *But in all cases the cycle is made up of stages of fusion or of segmentation between the two extremes of one single nucleolus and of numerous granules.* (The law is unchanged even if we suppose that the granules are the nodes of a reticulum.) Usually nuclear division follows that point in the cycle where the chro-

matin is most condensed. Thus, even in the Remakian schema, this law is followed, as see Figs. 99, 100, 101. *Cases like Figs.* 101, 103, 104, *and karyokinesis in Metazoa are related to the Remakian schema by a compounding of the latter, for each karyosoma follows the Remakian schema.* We thus see that direct division is to indirect division as a unicellular or unisegmental animal is to one that is multicellular or multisegmented. *If we study the cell-division of multinuclear Protozoa we find that the same laws hold.* Opalina is an exception, and such forms as Polykrikos (Fig. 96), that have only nuclear division during cell-division, are connecting links to the far larger class of cases, where, as in Oxytricha (Fig. 95), Paramœcium (Fig. 97½), Stentor, etc., there is fusion of the nuclei (or of nuclear segments in moniliform endoplasts) before division and multiplication of these bodies preceding, during, or following division. In Paramœcium the resting phase concurs with the mononucleate phase. But even in the exceptions to this law there is fusion, when these forms encyst to produce spores (Fig. 97) by the successive or by simultaneous division of the fused nucleus. In such cases, as in conjugation of low forms, the phenomena may be facultative, the number of nuclei resulting from the fusion being one which varies from one to the original number, just as the resulting spores may vary in number.

What is the meaning of this? *It is evident that we have here to do with conjugative phenomena.* These self-same nuclei that with one form of cell-division fuse, may, in case of buds, be set free, as microgonidia to fertilize other gonidia. It may be that the granules and nuclei are in different parts of the cell subjected to different conditions, and thus come to vary slightly. If, now, the cell divided, the daughter-cells would differ, and ultimately new species be formed. But, as we find that if conjugation phenomena be left out in one place in the different modes of reproduction it is apt to occur in other points of the cycle, and if prevented, as in male and female parthenogenesis, the resulting organisms are weak, we must conclude that the organism derives some benefit from the mixture of chromatins that are slightly different. In the case assumed above, where cell-division is not accompanied by fusion of the nuclei, we may presume that conjugation of gametes supplies this lack,[1] though in Opalina the only

[1] The formation of varieties and species must take place in spite of this tendency of differentiated chromatins to fuse.

form of fertilization as yet discovered is that of nuclear fusion during encystment. But Opalina is a parasite, and parasites, we know, get along remarkably well without fertilization.

This explanation of karyokinesis seems quite plausible, so that we may formulate the law *that every cell-division is preceded by fertilization phenomena: is accompanied by close inbreeding.* Other explanations have been suggested. Strasburger regards karyokinesis as resulting in like cells, therefore the different chromatins present must be carefully divided, so that each daughter-cell shall receive its proper ingredients. Roux and Weismann go further and call attention to the fact that dividing cells are not alike, so that we need a particular distribution of the gemmules for each division, so that, to follow the last author, in the first egg-segmentation, the histogenic plasm is separated from the generative plasm. Thus the soma is descended from one blastomere and the generative cells from another. In a similar way the endoderm-cells have a common ancestor, and the ectoderm another, and so on. This explanation seems to me difficult of application to the Protozoa, so that the law enunciated above appears to be unaffected.

3. *General.*—It would extend the length of this paper unduly, as well as be of no interest except to the specialist, to discuss the various views that have been advanced in interpretation of the special stages of karyokinesis. Nevertheless, some of the more prominent features should be noticed. We have already seen that cell-division need not be necessarily associated with nuclear division, whether this be direct or indirect, so in the higher tissues there occur cells that present such conditions. These are the internodal cells of Chara, many fungi where the nuclei are granules, and the generative tissues of both plants and animals; also in cartilage-cells and marrow-cells. In the generative tissues of plants cell-division does not take place until many endosperm nuclei are present, and to this form of division the term *free-cell formation* has been applied, while the term in the sense in which Schleiden used it has been pretty nearly abandoned. Still, we saw that in the Protozoa nuclei could arise by the fusion of granules, and return by fragmentation to the granular state, and it may be a question whether similar phenomena may not be found in tissue-cells. The cases of the endogenous origin of nuclei are

reported in eggs that have so much yelk that it is hard to follow the nuclear changes.

Does the cytoplasm or the nucleus stimulate division? Hertwig holds that the nucleus is the automatic centre which controls the individuality of the cell, but it must be confessed that the earliest changes are in the cytoplasm. Protoplasm gathers at two points and forms stars, between which the nucleus becomes stretched out and transformed. Carnoy (Fig. 124), and lately (1886) Hertwig, have found independent stars arising in the cytoplasm, and if more than two of these get connection with the nucleus, there are as many poles and spindles or resulting daughter-nuclei as there are asters. The rays about these asters are simply a transformation of the reticulum. What their function is we can only guess with the numerous guesses made by predecessors. They may be nutritive, may be paths for travelling gemmules, may have a nervous function, or finally only serve motor functions. The spindle-fibres are a similar transformation of the nuclear reticulum (*i.e.*, the parachromatin reticulum); whether the nuclear membrane in dissolving adds to their material, or gathers at the poles of the spindle as in Actinosphærium, ~~may be~~ is doubtful. In the latter case it would continue its original function of mediating between the intra- and the extra-nuclear reticulum. But Strasburger and others find that the astral- and spindle-fibres are continuous, and thinks the latter come by a penetration of the former through the poles of the nucleus. But the mass of evidence is against him, and besides, the spindle-fibres are composed of parachromatin (chemically, *plastin*) and react differently from the extra-nuclear fibres.

Then there are the polar corpuscles in the centres of the stars, and forming the apices of the spindle. Their origin is obscure. Possibly the plastin nucleolus of Carnoy may, by its division and migration, have initiated the division of the nucleus, and is represented in these corpuscles. It is certain that these corpuscles may divide, and so split the spindle (Fig. 124), and often the two stars first arise close together, and move later to opposite poles. We must also notice Rabl's discovery of a spindle intact in the nucleus, which rotates into its position (see Fig. 113, *c*) through an angle of 90°.

In what condition is the chromatin in the resting nucleus? It may be present as a fine or as a coarse reticulum, closely inter-

penetrating the parachromatic reticulum, and perhaps fused with it. In the germinal vesicle it is present as a nucleus, which becomes transformed into the reticulum before division. The next change this reticulum suffers is its transformation into a mitom,—*i.e.*, a filament,—which, while it is very long and closely balled up, may not be distinguished from a reticulum. Some nuclei rest in this phase, or in subsequent phases of its shortening and consequent thickening. When thick it has been found to be composed of granules that fuse to form microsomata, so that finally the mitom is one microsoma thick. The next phase is one in which the mitom segments into loops or filamentous karyosomata. Some cells rest in this phase. (See Fig. 124.) When the segmentation occurs early, while the reticulum is being transformed into the mitom, we get a condition of things represented in Figs. 113 and 45. The karyosomata are apt to be short or corpuscular in generative cells. (See Figs. 122 and 123.)

Now we have two ways in which the karyosomata are separated into two groups to form the daughter-nuclei. In one they are separated without accompanying division, as in Fig. 124. In the other they divide in such a way that each half of the karyosoma is destined to pass into different daughter-nuclei. In this case we get two forms. In one form the karyosomata, if they are short, become arranged into a nuclear plate in the equator of the spindle, and by division and separation of the halves we get two daughter-plates that pass to the poles, and become the daughter-nuclei, but if they are long, they lie along each spindle-fibre and are bisected in the equator as in Figs. 101 and 115. In the other case the daughter-segments are produced by a longitudinal splitting of the loop, as shown in Figs. 114, 118, and 119, in which splitting usually occurs early, while the spirem figure still persists, and in this case no true equatorial plate may form, but be only the expression of separating loops passing each other on the way to their respective poles. Between all these different methods there are connecting links. Carnoy calls such a case as is seen in Fig. 109 *stenotic* division, while similar separation with more complex spindle and asters, as in Fig. 124, he terms *cytodieresis.*

Finally, the karyosomata reach the poles and pass through stages of fusion of the larger bodies and segmentation of the smaller, so that the nucleus appears homogeneous because of its

very fine reticulum. Then from this point the changes continue along the upward path to the resting phase, wherever that may be. While undergoing this fusion, the hyaloplasm in which the chromatin-granules are imbedded become much increased, so that if the chromatin is sparse we get vesicular unions, like Fig. 125. This hyaloplasm is parachromatin, and it undoubtedly enters partly into the formation of the spindle-fibres; in Fig. 126 appears to be the only source of these.

Concerning the nucleoli that may be present, besides the reticulum or mitom and the plasmatic nucleolus, there exist the most diverse views. In the first place, we must call attention to the fact that very diverse structures have received this name by different writers. The nodes of the reticulum, the karyosomata, the groups these may form when unresolved by the lens, all have received this name. The "true" nucleolus seems to disappear during division, and to be gradually built up by fusion of granules at its close. It has been supposed that it dissolved in the nuclear sap, and was absorbed by the mitom, or that it was directly connected with the mitom, and so incorporated into it. Thus Pfitzner called its substance *prochromatin*, as being a store from which the mitom replenished itself, but has lately changed the name to pseudochromatin, and other authors think it is of accidental value. Those who think with Strasburger, Fraisse, Kassel, and Brass that the chromatin is food-substance and the hyaloplasm the real idioplasm, find no difficulty with this body. But it must be remembered that it also has hyaloplasm, so the difficulty is unsolved. What is the meaning of those polar corpuscles (not to be confounded with the polar corpuscles considered above) seen in Fig. 112, *c*, *o*, *d*, which multiply as the loops multiply, and whose number is approximately two or three times that of the loops? It almost seems as if they were related to the karyosomata, as the endoplastules of Protozoa are to the endoplasts. They may have come by the segmentation of the nucleolus, and in that case this body is a paranucleolus over against the mitom. But these bodies may have come from the plasmatic nucleolus of Carnoy, and so we are still in doubt.

Another unsolved problem is concerning the connecting fibres that remain between the retreating karyosomata. In plants they help to build the cell-plate, and the nucleus gets reconstructed without their being absorbed. In animals they seem to be ab-

sorbed, for, if left outside, they form the paranucleus of Platner (see Fig. 123), which is later absorbed by the nucleus to form the spindle. They are thus made of substances similar to those which enter into the parachromatic reticulum, and, when not absorbed by the nucleus, they join the other fibres of the cytoplasmic reticulum, from which they can no longer be distinguished. Thus the chromatin of the nucleus must make more hyaloplasm, from which a new parachromatic reticulum can arise.

There is some evidence of the existence of microsomata that are not chromatin; in the cytoplasmic reticulum these are not so active in their fusions and segmentations as the nuclear microsomata, but still they do this, for the spindle-fibres and rays, when extra-nuclear, have been observed to segment and fuse. This can easily be understood by combining with Heitzmann's schema the idea of units in the cell. Strasburger and Pfitzner recognize the microsoma as such a unit, and we have shown that there are numerous units of differing complexity and degrees. When two organisms differ in the number of units that enter into their structure, such difference is one of degree in the ordinary sense, but when two organisms differ by belonging to higher or lower stadia of organization, such difference constitutes a *discrete degree*. Such degrees separate the Protozoa from Metozoa, a man from the social organism, a cell from the microsoma, a microsoma from a gemmule. Though here further study is needed to discover the number of stadia visible to the microscope, Nägeli has admirably discussed the stadia that lie between the chemical molecule and the micellæ, and Altmann has suggested that the bacterial organisms are of the same grade of organization as the microsoma. *Each node in a reticulum may be conceived as a unit.* We have already seen how, when chromatin segments, it may leave a funiculus of hyaloplasm (with or without a wall). This connecting piece of hyaloplasm may break by being drawn towards the centres on either side of it, or it may, like a pseudopodium, reach out and obtain a fresh connection with a neighbor. This is admirably illustrated in Fig. 123. In this way it is *that a reticulum can be transformed into a mitom or a fibre.* The observations of Rabl and of Retzius on the formation of the mitom become intelligible. By the attraction of the hyaloplasm along definite paths, and their separation along others, we may also see how a

nucleus arises in a cell, as in Fig. 2. By mutual attraction the microsomata fuse. Why they segment may be explained by assuming that certain gemmules or societies of gemmules differentiate from the others and serve as governing centres, about which the rest flock. Individuality arises in this way everywhere. The cause of union between two units of like order, which constitutes sexual union, is not so apparent. We find this occurring only where a slight difference has arisen, so that, Lankester says, "they may mutually gain each other's experience." At bottom all the phenomena of the cell-life may be referred to attractions, and through its action the reticulum becomes the organ of movement.

There is considerable evidence that successive cell-divisions differ in their karyokinetic phenomena. We know that the number of karyosomata in the segmenting-egg are fewer than in the tissue-cells, and that they are shorter. There must be a change somewhere. But in gametogenesis two successive generations may differ, as can be seen by Figs. 123 and 124. We may start in gametogenesis with direct division, pass on to generations produced by budding or by stenosis, and finally reach the complex phenomena of the segmenting embryo. We know only a little about this. Our knowledge compares with what we should know, as the knowledge of zoologists, before embryology, compares with their present knowledge. When we reflect that we must observe cells in all periods of their life and all the generations of cells as they differentiate, and we must do this for all the different animals, and the results must be corroborated by different observers, morphologists need not quarrel for lack of room nor sit idle for lack of work. We can also understand why karyokinesis is such a mysterious phenomenon. *Cell-division must be understood ontogenetically and phylogenetically.*

(*d*) FERTILIZATION.

Fertilization, fecundation, copulation, conjugation, zygosis, are some of the terms used indiscriminately when referring to the fusion of sexual elements. We may refer to the *fusion* of nuclei, or of cells; or simply to the *apposition* of cells, or of individuals for sexual purposes. We shall use the term *conjugation* always in the former sense and *copulation* always in the latter. Thus we shall use the term *copulation* where other writers say

"temporary conjugation." Conjugation of cells when not followed by conjugation of the nuclei produces *plasmodia;* we might use the term *zygosis* when fusion of the nuclei is involved. *Polyspermy* is where more than one male cell fuses with a female cell; and *superfecundation* implies, or should imply, the conjugation of more than two nuclei to form one *zygote.* We need one term more, and that is where, in polyspermy, the female nucleus segments by stenosis to furnish a partner for each of the male nuclei. For this case we would suggest the term *multifecundation.*

The modern theory of fertilization dates from the birth of the cell theory, when Kölliker extended its scope by advancing the view that the spermatozoon is a cell, and that it fertilizes the egg by a fusion with its substance, as against the theory that it was the fluid portion of the semen which holds the impregnating power. This view was not established until 1847, although Barry had seen the spermatozoon penetrate the ovum in 1843. It was now possible to compare fertilization with the conjugation which successive years of study continued to discover in the different groups of plants and animals, but with this line of development we are not here concerned.

In 1827, Baer described as *maturation* of the ovum the changes which the egg nucleus suffers, and Purkinje three years later named this nucleus the *germinal vesicle,* because it bursts and lets out its "generating lymph" through the germ. Attention was first called to the polar globules by Dumortier, and Müller named them *direction corpuscles* in 1848, because he thought they fixed the plane of cleavage. It was in 1862 that Robin gave them the name they now usually bear.

In 1842, Bischoff saw the germinal vesicle expelled from the egg during maturation, and this was confirmed by other observers, and thus the idea that the polar globules were the extruded germinal vesicle was gradually established.

In 1853, Keber discovered the micropyle, and the theory of actual penetration of spermatozoa into the egg thus received more favor, speculations concerning the functions of the spermatozoon became more numerous. Bischoff held the katalytic theory, by which molecular motion was supposed imparted to the egg through the spermatozoon. Meissner thought it was a nutriment, others thought it served to help maturation, and thus

for a long time the formation of polar globules was supposed to depend on fertilization. The independence of these phenomena was shown in 1875 by Hertwig.

The penetration of more than one spermatozoon was seen by several observers, and it was only gradually that the idea gained ground that normally but one spermatozoon enters the egg. Perez thought, in 1879, that there may be degrees of parthenogenesis, so that if this is strong in tendency, it does not take as many spermatozoa to saturate the ovum as if weak.

The next step was the discovery of the sexual pronuclei. The male pronucleus (so termed by Fol) was first seen by Weil in 1873, but its direct morphological connection with the head of a spermatozoon was first established by Hertwig in 1875. Hertwig also showed that the whole germinal vesicle was not extruded in the polar globules, but that the germinal dot remained to be transformed into the female pronucleus, which fused with the male pronucleus. Auerbach had seen these pronuclei fuse, but supposed they originated in opposite poles of the egg, and by uniting, the characters of the different hemispheres of the egg would be mixed. Beneden and Bütschli practically saw the same thing later, but likewise derived these bodies by endogenous formation. Fol was, however, successful in seeing the female pronucleus derived from the amphiaster which extruded the polar globule; but it remained for Hertwig, in 1877, to show that the polar bodies arise by a true karyokinetic division of the egg-nucleus, and are thus the homologues of the female pronucleus. Bütschli and Giard arrived at this result independently.

Then Whitmann was enabled to give what we consider as the true theory of the polar globules,—viz., that they represent an asexual generation of cells that once were functional.[1] Beneden, Minot, and Balfour carried this view so far as to say that the polar globules are male cells. Thus, that every cell is hermaphrodite, having male and female plasmas, and that the cells become sexed by extruding one of these plasmas. It can then no longer develop until it has fused with a cell containing plasma opposite in character to itself. The absence of polar globules in any instance does not disprove the theory, for this plasm may be gotten rid of in many different ways. But this

[1] Bütschli said the polar globules are to be considered as the first stages of development due to fecundation, rather than due to maturation.

theory has lately received its death-blow by the discovery of polar globules in parthenogenetic ova. Strasburger has modified the theory by his idea that the nucleo-hyaloplasm is primary idioplasm, while the cytohyaloplasm is secondary; the former is conservative, the latter is adaptive. Cell phenomena are due to a dynamic interaction of the two. Two nuclei may be alike, but because the cytoplasms differ the cells will develop in a different manner. Cells become sexually mature, therefore, by getting rid, by division or any other way, of certain constituents in the cytoplasm.[1] Weismann says that these constituents are histogenic plasm,—*i.e.*, plasm which belongs to the cell as a cell,—and when this is lost then the plasm, which represents the generation of tissue-cells to come from the segmenting egg, may develop. A view similar in some respects was advocated by Robin in 1875.

It is strange how many different bodies, having not the slightest homology, have been appealed to to prove the sexual nature of protoplasm. Every sort of paranucleus has been worked into line with this theory. We have already adverted to the fact that paranuclei are themselves very different bodies. Thus, in Fig. 49, Gaule's paranucleus can be homologous only with the germinal dot of the (parthenogenetic) ovum; for from it the new cell develops, while the old nucleus goes to the ground. Besides paranuclei other things have been supposed to represent the lost sexed protoplasm, such as canal-cells, perivitelline excretions, synergid-cells, follicle-cells, nutritive cells, seminal granules, "remains" ("Rest") of protoplasm in spore formations, and, in fact, any sort of excretion and secretion. Trouble arises in explaining cases where more than one of these modes coexist. Thus, Sabatier holds that in gametogenesis one cell buds off a number of cells, which become nutritive to the mother-cell, in the ovary; while in the testes the daughter-cells develop to spermatozoa at the expense of the mother-cell. Such a theory as this cannot possibly be universally applied, and does not explain polar globules. Our knowledge of sex has developed by two steps more. Beneden showed in ascaris that the two pronuclei are just alike, each containing two loops that are placed in order in one equa-

[1] The idea of Fol is that certain substances injurious to further development must be excreted. This is only a general statement of the fact that cells must accomplish a certain cycle of work before they are sexually mature, most commonly a certain number of divisions.

torial plate in the zygote, and split as in ordinary karyokinesis, to furnish the two daughter-nuclei. (See Fig. 124, *l–o*.) In the latter the four loops reappear as a result of the process of reconstruction, so that Beneden thought that each daughter-nucleus had still two male and two female loops; and thus every cell of the body may be considered hermaphrodite, having the chromatins of the two sexes in morphologically distinct structures; and finally, when any cell becomes sexually mature, all that happens is a cell-division at right angles to the ordinary cell-division, thus separating the male from the female chromatin. But this theory is very faulty, for in the first place the phenomena of karyokinesis have as one object the mixture of the chromatins, and we know that this is accomplished in one phase or other somewhere between two successive divisions. Then, secondly, the chromatin derived from the spermatozoon possesses the characters of its ancestry, both male and female; if this be lost the characters which fertilization has bestowed are lost; and as this loss occurs with every generation, how could there ever be an accumulation of characters?[1] Only through the idea that chromatin is sexed can such grave errors as this arise. Platner (see Fig. 126) furnished an important contribution when he showed that in Arion the number of microsomata derived from the male pronucleus is less than a fourth as great as that of the microsomata in the female pronucleus. Thus the two pronuclei bear the relation of macrogonidia and microgonidia to each other. In Limax the microsomata are approximately equal in number in the two pronuclei; and as the result, so far as fertilization is concerned, is the same in the two animals, we must believe that the pronuclei need not be morphologically equal. It has been said that the two parents furnish equal contributions of hereditary characters because the chromatin is alike in amount in the two pronuclei. But this assumes that quality depends on quantity. We cannot accept this notion. We believe the quality of the chromatin inheres in the nature of each gemmule, that the gemmules are nearly alike, and that the quantity of chromatin may readily be increased by the multiplication of the gemmules. Such multiplication may take

[1] Strasburger holds that the contributions of the ancestors in each fertilization remain distinct in different parts of the mitom. Roux, in a somewhat analogous way, thinks that each portion of the egg-plasm corresponds with a definite portion of the soma that develops from the egg.

place in the male pronucleus before fusion because of the nutritive conditions furnished by the yelk. Even if it did not increase in this way, it might happen that the reproductive vigor of the fertilizing gemmules is so great that during ontogeny they would at last outnumber the ovum gemmules. We do not know whether characters are realized in proportion to the number of the gemmules, or whether it depends on the strength of the gemmules, or, again, on some dynamic influence reciprocally acting between the gemmules. In the last supposition we might have each gemmule possessing a system of vibrations whose wave-form could be slightly altered by the proximity of differing systems; and that, finally, equilibrium being established, it would require a new fertilization to introduce a new variation. It would also be intelligible how gametes may develop parthenogenetically before fusion is accomplished where only the preliminary steps to such end have been taken. Finally, such variation could be effected by other means than by fertilization.

Under the first supposition we could understand how, if cell-division should not succeed in separating the gemmules in due proportions, we might get cells that had a preponderance of gemmules of one ancestor, and the parts of the body developed from the offspring of these cells would present the characters of one parent to the exclusion of the other. But we defer the discussion of this point to the subject of heredity.

Strasburger claims that fertilization is effected by the fusion of similar parts in two cells, cytoplasm with cytoplasm, nucleus with nucleus, and nucleolus with nucleolus. But in phanerogams it is only nuclei that migrate from the pollen-tube to fuse with the egg, and in many animals it is only the head of the spermatozoon that makes the male pronucleus, the greater part of the flagellum not even getting into the yelk, so that we are justified in believing that fertilization is essentially a phenomenon of the mixture of chromatins. We cannot speak even of the union of "half nuclei" to make a whole nucleus, nor say that the nuclei are morphologically alike, nor yet that they are the *complements of each other* in any way. That the sexual pronuclei are physiologically alike we may infer from the fact that the characters of both parents are equally well transmitted, and from the fact that we may get both male and female parthenogenesis, which latter statement receives its best support from the evidence afforded

by polyspermy and by the behavior of unfertilized eggs. We know that, aside from differences in size or in locomotor organs and other secondary characters, gametæ may differ physiologically in this way: in one, which we usually call the male, or microgamete, there has been a greater number of cell-divisions than in the female gamete, but in the latter we may, by enforced parthenogenesis, secure just as many divisions, and so make the cells alike. But neither of the gametes have divided as many times as they can, for it is possible, though more difficult than with the ovum, to get male parthenogenesis. The offspring thus resulting are more sexed, have greater desire as well as need for fusion with other cells, especially cells that have not divided as much as themselves. Unless we give such cells easy conditions of life we reach a stage when they can no longer divide. Such facts as these, observed with spores and the protoorganisms, enable us to understand certain phenomena obtaining with fertilization in higher forms of life.

We should expect that in most cases the ovum would possess a tendency to segmentation, which is realized normally under conditions of easy nutrition in parthenogenetic development, but may be realized in a less degree with other eggs. As a matter of fact there have been a number of observations in widely different groups of animals that show a sort of irregular segmentation of unfertilized eggs. I have observed such cases not infrequently. Such segmentation is slow and irregular, and probably cannot proceed as far as normal segmentation. Von Jhering saw the female pronucleus form an amphiaster in unfertilized eggs. Schneider, Greeff, Oellacher, and others have reported development in unfertilized eggs. But this phenomenon has not received the attention it deserves.

In polyspermy we find that not only does the female nucleus form an amphiaster, either alone or by zygosis, with one male nucleus, but that the male nuclei left unconjugated also form amphiasters. This phenomenon was first studied by Fol, 1879, but Hertwig has just published an article fully illustrating these forms. If more than one spermatozoon conjugates with the female nucleus it develops a tetraster (sometimes a triaster), or a figure having a greater number of poles according to the number of spermatozoa fusing. It results that segmentation follows a series whose terms are multiples of the normal one. But this

only when there are no free spermatozoa in the yelk, for in such a case each of these also segments and receives its bud of cytoplasm, thus making the segmentation of the egg irregular. When the nuclei fuse before the spindle is formed, the number of spindles seems to depend on the number of nuclei. (This may be doubtful, as the poles seem to be determined by asters independently arising in the yelk, which migrate to the nuclei and direct their transformation.) But the amphiasters and the more complex tetrasters, etc., may also unite among themselves, regardless of sex, by superposition of poles, thus building up complex figures that may be as regular as a dodecahedron. The result is the fusion of daughter-nuclei of diverse origins. It follows, therefore, *that the spermatic nuclei after one segmentation have an affinity for each other.* Hertwig found further, that the nuclei resulting from the segmentation of pronuclei became fused again, but whether there was subsequent division and normal development remains an obscure question. The male nuclei also form triasters and tetrasters which cannot be distinguished from those made by the female pronucleus; but it is possible that in these cases multifecundation has taken place. Besides Fol and Hertwig, polyspermy has been studied by Bergh and Horst, 1881, and by Strasburger in phanerogams; Salenka and Schneider report normal development as following polyspermy; but this subject also requires further study.

Another line of study has been followed by Hertwig. It is well known that certain nuclei which are not too closely nor too distantly related to each other are prepotent in zygosis above these others, and that the egg resists the entrance of foreign spermatozoa. By letting the eggs lie a long time in impure water Hertwig has so weakened this resistance as to effect hybridization between forms not ordinarily capable of being thus hybridized. But as he got results closely similar with unfertilized eggs and also with eggs where polyspermy of its own species took place, and furthermore, that polyspermy ensued in these cases of enforced hybridization, we must be cautious in our inferences. To leave eggs a long time unfertilized, instead of developing the tendency to fuse with any partner, ought rather to develop the opposite or parthenogenetic tendency. Strasburger thinks superfecundation arises when the gametes are not sexually mature. But here again we have no thorough knowledge of the facts. Spermatozoa

have also been seen to penetrate the polar globules, which is not remarkable, as we know that these are (when the first globule has divided again) the counterparts of the female pronucleus; but Hertwig found that the spermatozoa penetrate any globule of extruded yelk (whether it has a nucleus or not) when artificially pressed out through a rift in the egg membrane. Probably, then, the attraction of the spermatozoa is for the nutriment, or for the cytoplasm, and the nuclear attraction arises later in accordance with other laws.

We see from this survey that sex in its primary sense, as inhering in the nucleus, or perhaps in Strasburger's sense as due to a peculiar stimulus of the cytoplasm upon the unsexed nucleus, sex is not an absolute condition but admits of degrees, is, in fact, a want, a hunger, which the cells may experience in different degrees. How the mixture of different characters confers vigor to cell-division we cannot explain. Perhaps we would be more general if we said that fertilization consists in broadening cell-education. Hence parasites that are cells of one idea do not need it to any extent. At present we cannot see how it is possible to explain it on physical principles. It is, however, only a confession of ignorance to refer the problem of heredity to the domain of psychology; we have explained nothing in so doing.

The Protozoa.—Here the phenomena of fertilization are very varied. In the lower flagellates more than two cells may fuse; and polyzygosis has been observed also in Actinophrys and Arcella. We must, with Lankester, also place in this category the formation of plasmodia and of the *syzygies* of Sporozoa. In these plasmodia, especially when encystment occurs, there may be a fusion of nuclei to a greater or a less extent before spore multiplication; and the same thing happens with multinucleated forms like Gastrostyla, Actinophrys, and Actinospherium. Multinucleated cells are not separated from plasmodia by any distinct line, for in Heliozoa, Greeff found that division of the cell is facultative and optional, following the nuclear division, and if it occurs, the cell-bodies are apt to fuse again. In low forms of Protozoa conjugation also is as facultative as with those protophyta, where both male and female parthenogenesis have been noticed.

We may get conjugation between ordinary zooids, or one of the gametes may be a microgonidium while the other, not having divided so fast, remains as a macrogonidium. Again, the gametes

may be due to spore formation; and here, again, the spores may be alike or unlike, and conjugation may be between like spores, or may be between macrospores and microspores. If the conditions of life are equal, the more often the cell-division has taken place the stronger is the desire and need of conjugation, so that where macrospores are parthenogenetic, microspores may be gametes. That this need of conjugation does not depend on the small quantity of idioplasm present may be gathered from two facts: first, when spore formation succeeds conjugation the resulting spores are smaller and more numerous than if parthenogenetically produced, but whereas the latter are apt to be gametes the former grow with vigor and multiply rapidly; secondly, where cell-multiplication allows time for the cell to grow as in ordinary gonidia, gametes are just as apt to form. In spore formation the microspores are not gametes more often than the macrospores because they are small, but because they have undergone division more frequently. In forms where both gonidial and sporular gametes occur, a failure to conjugate in the gonidial stage insures conjugation of the spores, while the occurrence of conjugation in the gonidial stage insures sporular parthenogenesis.

The Vorticellæ enable us to understand that fertilization has to do with quality of the gemmules and not with the number of these present. Two zooids which have resulted from the repeated division of a mother-zygote and standing near each other bend together and conjugate. But others just like these bud off a piece of the nucleus with some of the cytoplasm, and this goes swimming away until it finds the appropriate gamete (a macrogonidium) with which to fuse. As the chance of cross-fertilization is greater in proportion to the number of these microgonidia, they have acquired the habit of dividing a few times after their separation from the macrogonidium before starting out on their search for partners. Here, as with Arion, a small quantity only of the idioplasm is needed to effect fertilization. We do not contend that there may not be some advantage in starting with a large quantity of idioplasm, but we do call attention to the fact that, compared with the vigor due to the mixture of idioplasms of diverse experience, such advantage becomes quite secondary.

We may now pass to the consideration of the phenomena of copulation. The simplest cases join easily on to the case last

considered. When the bud from the nucleus is not carried away by cell-division it may still be transferred to the interior of another cell, if such cell be brought with an aperture close to a corresponding aperture of its own cell. When the nuclear bud is produced at the time of the fertilization, Engelmann terms the gametæ "periodic hermaphrodites" (so far as this implies sex it is a misleading term). When, however, the nuclear bud remains as a permanent endoplastule and does not conjugate with the endoplast, except perhaps for a brief period in connection with fertilization, after which it is immediately budded off again to form the endoplastule, then Engelmann calls such a cell a "permanent hermaphrodite." In some cases the whole reproductive function may have passed over to the endoplastule, so that this never conjugates with the endoplast, but rather by its own division builds up the latter when this disintegrates. Periodic hermaphrodites are Stentor, Spirostoma, and Trachelius; while permanent hermaphrodites are Stylonychia, Euplotes, and Paramœcium.

Copulation is most frequent with the Ciliata, but has been observed in Peridinium and in one-chambered Rhizopods. An alternation of copulation with conjugation occurs in Stylonychia and in Platoum (Troglodytes). See Gabriel.

In connection with conjugation and copulation there is in all the higher forms a segmentation of the nucleus, or of the endoplast and endoplastule respectively. The last leads in the division, but is not divided up so finely as the endoplast. The phenomena are closely similar to those that accompany division. The cycle of segmentation and of fusion is passed through, so that the foreign idioplasm becomes incorporated into the nuclear structure. Possibly it does not get thoroughly mixed with the nuclear idioplasm in a molecular or rather gemmular intimacy, but as this process of segmentation and fusion is repeated for each division, there is no reason to suppose that after a while this may not be attained. Thus it is that *every cell-division is a fertilization.*

In the conjugation of Stylonychia, there is a fusion of nuclei with nuclei across the body, first uniting the nuclei of the two gametes; and then the anterior nucleus (zygote) fuses with the posterior one, after which the two nuclei are reconstituted. Possibly, Engelmann says, the nucleoli (endoplastules) do likewise. In copulation of Stylonychia there is segmentation of the nuclei

and probably of the nucleoli, but Engelmann was unable to observe any transfer of material between the gametes. The nuclear fragments fuse to one body and bud off the nucleoli, but here there is disagreement, for in another case it seemed as if the nuclear products were extruded (Bütschli), the nucleoli became four in number, one disappeared, two became the new nucleoli, and the fourth, dividing, formed the endoplasts.

In copulation of Anoplophrya, Schneider could not observe any exchange of nucleoli, but the nuclei sent processes into the apposed cell, which became budded off mutually and fused with the remnant of the original nucleus to form a new nucleus, while the nucleolus came from one of the four segments into which the nucleolus divided; the other three disappeared. In Paramæcium, the endoplastule and the endoplast get segmented, the former usually into four, the latter into many, granules. Then there is a fusion of the fragments, but as to how this is done, and as to whether there is any mutual interchange of idioplasm, is a question which has received a dozen different answers.

Greeff thought the nucleolus was a semen capsule and the nucleus an ovary. The "eggs" that came from the "ovary" being fertilized, developed to living embryos viviparously. Stein called that part of the nucleus which remained after budding off eggs the "placenta," Balbiani, that the eggs were laid, and Engelmann also, with many other early observers, held views of a similar nature, according to which we had here a true hermaphodite. Engelmann subsequently modified his views to some extent, but Bütschli attempted to bring the phenomena into line with his observations on tissue-cells, and so he held that the nucleus is extruded, due to fertilization, and a new nucleus arises endogenously, and this is *rejuvenescence*. In 1882, Balbiani showed that there was an interchange of nucleoli; and Jickeli, in 1884, saw two nucleoli in the act of passing each other across the line separating the gametes. Lankester could find no interchange, but said that a portion of the segments of both bodies are lost, the remaining ones fuse to constitute the new nucleus and nucleolus, but *with reversed functions*. (See Fig. 128.)

Maupas, in 1886, said all the products of the nucleolus are lost except one; this divides, and one daughter remains and one crosses to the other gamete to fuse with the stay-at-home over there. The resulting zygotes segment to eight daughters; of

these, three are absorbed, four become nuclei, and the eighth, after repeated divisions accompanying cell-division, becomes four nucleoli. The old nucleus is absorbed. Plate, in the same year, saw no interchange, but did see two nucleoli in apposition with a wall between. Gruber, however, saw the same thing, but no wall between, so that there was a chance for some interchange of substance. There was no fusion, however, for the nucleo-gametes separated and returned to divide into four. Gruber thinks the "stay-at-home" nucleolus acted in a similar way, for eight nucleoli result, and four of these fuse to form a new nucleus, the other four fuse to make a new nucleolus.

Truly, when such eminent observers disagree, who can decide? For our present purposes it is sufficient to know that there is an interchange in this case as in all others of fertilizing material, and that this is mutual and reciprocal. We cannot here, as did the older observers, speak of male and female idioplasm. That the functions of the endoplast are different from those of the endoplastule is evident, but Weismann claims that the reproductive plasma is restricted to the latter, while the former has only histogenic plasm. Thus, from a survey of fertilization in its relation to the nuclear phenomena, have we been enabled to get pretty clear notions of the significance of sex. But our morphological inquiry would not be complete did we not study the various methods of cell reproduction and observe the relations of these to the production of gametes. Several of the laws discoverable through such a survey have already been anticipated, but others will appear that are needful to the proper comprehension of the significance of sex.

Briefly, then, in conclusion, we have shown that the phenomena of life are the manifestation of forces that are organized, by being in some way connected with an ultimate unit, which unit, by multiplying and differentiating, forms units of a higher order; and these units repeat the same process, and so we get higher and higher units capable of a more complex life. Only in this way is organic life connected with inorganic life. A series of discrete degrees separates such life, as we study with the lens, from the substances with which the chemist deals. We can study the higher stadia morphologically, and only by analogy do we guess concerning the nature of the lower. We find the cell a reticulum of hyaloplasm holding microsomata in its nodes as nuclei.

We find the soma of a metazoon likewise a reticulum in which the cell is the unit. As in the body, all cells come from embryonic or germinal cells, all traceable back to a single egg, so in the cell, all the differentiated gemmules, or micellæ, or tagmata[1] are descended from nuclear idioplasm, which is itself due to the multiplication of a single gemmule. Finally, we find that cell phenomena are accompanied by fusion or mixture of idioplasms that have had diverse experiences, and in some way the cell-life is thereby invigorated. Sex has been evolved as the means of effecting such fusions. The distinction of male and female has arisen comparatively late and is coupled with very secondary characters.

We have seen that half a dozen different structures are present in the cell, and that those in the spermatozoon are transformed into the different parts of its structure. Undoubtedly in the metamorphosis of all tissue-cells these structures play a part. If we could see which of these structures preponderates in a given tissue or organ, we could infer that the function of this part is similar in the cell to the function of the tissue in the soma.

Gaule's work on the cytozoan, or paranucleus, which can wander from cell to cell, and on which the cell-life depends, is yet too little known to be criticised. We may expect fuller details when Gaule has completed his researches.

LITERATURE BEARING ON THE SIGNIFICANCE OF THE CELL-NUCLEUS TO THE PROBLEM OF SEX.

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[1] The ferments such as zymogen, etc., which are lower in the scale of organization than the bacteria, seem to come in somewhere near the plane occupied by the *gemmule;* but their relation to the latter is probably at present beyond the scope even of a guess.

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NOTE.—The substance of what has been published under the head of Significance of Sex was originally delivered as part of a series of lectures in the spring of 1886, from random notes. In preparing the article for publication I have added historical matter and the latest literature, but the plates having been first prepared, do not contain, as they otherwise would, some of the instructive figures which accompanied this later literature.

JOHNS HOPKINS UNIVERSITY, March, 1887.

ERRATA.

On page 4, line 10 from bottom, read "constricted" for "constructed."

Fig. 56*a*, Plate III., should show a paranucleus which failed to print in lithographing.

THE SIGNIFICANCE OF SEX.

EXPLANATION OF PLATES I—IV.

The figures have been selected to show as great a variety as possible, that the unity which can be discovered may be a generalization of value. For the sake of clearness they have been drawn with as little elaborateness as possible, and to that extent are diagrammatic.

The following abbreviations have been used:

Z. w. Z.—Zeitschrift für wissenschaftliche Zoologie.
M. J.—Morphologisches Jahrbuch.
Carnoy.—La Biologie Cellulaire, 1884.
Bütschli.—"Protozoa," in Bronn's Classen und Ordnungen des Thierreichs.
A. B.—Archives de Biologie—Beneden and Bambeke.
A. m. A.—Archiv für mikroskopische Anatomie.
A. Z. E. G.—Archives de Zoologie expérimentale et générale.
Kent.—Manual of Infusoria, 1881.
M. z. S. N.—Mittheilung aus der zoologischen Station zu Neapel.
A. A. P.—Archiv für Anatomie und Physiologie.
Flemming.—Zellsubstanz, Kern, und Zelltheilung, 1882.
Q. J. M. S.—Quarterly Journal of Microscopical Science.
A. z. z. I. W.—Arbeiten aus der zoologisch-zootomisch Institut zu Würzburg.
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PLATE I.

FIG. 1. *Actinosphærium Eichornii*—Gruber,[1] Z. w. Z., xxxviii.—The protoplasm is in the form of a net-work with enlarged nodes, many of which bear nuclei in various stages of karyokinesis.

FIG. 2. *Calcarina spengleri*—Bütschli, M. J., xi.—A nucleus surrounded by reticulated protoplasm is shown. It contains one large and several small nucleoli, all

[1] The name following the species refers to the author of the paper from which the figure was copied, and does not necessarily refer to the discoverer of the species.

having essentially the same reticulate structure. Some of the nucleoli are dividing by simple constriction.

FIG. 3. *Intestinal epithelium cell* of an *insect*—Carnoy, p. 190.—The reticulate nucleus is slung by a fine net-work, whose radial trabeculæ are the more pronounced; they branch towards the periphery of the cell.

FIG. 4. *Intestinal epithelium* from an insect larva—Carnoy, p. 195.—The granules in the cytoplasm have been indicated in some sectors, and the reticulum in others. The heavy nuclear reticulum, containing the chromatin, has contracted under the action of the *chrom aceto-osmic* mixture of Flemming, and reveals a fine reticulum of achromatic protoplasm otherwise obscured by the presence of the chromatic reticulum (or filament, as the case may be).

FIG. 5. *Giant-cell* from marrow of rabbit—Carnoy, p. 262.

FIG. 6. *Encysted Vorticella*—Carnoy, p. 261.—In *b* the nucleus has divided into four.

FIG. 7. Nucleus of *Stentor polymorphus*—Carnoy, p. 260.

FIG. 8. Nucleus of *Monas vivipara*—Bütschli.—Microsomata of various sizes are united by processes so as to form a regular net-work.

FIG. 9. Nucleus of *Ceratium tripos*—Bütschli.—One of the nucleoli has an internal reticulum; the other is vesicular, having only a *surface* reticulum.

FIG. 10. Nucleus of *Ceratium tripos*—Bütschli.—No nucleoli present. *a* is an optic section from the side, *b* is a view of the ventral surface. The microsomata are strung in a row on each of the dorso-ventral filaments.

FIG. 11. Tentacle of *Noctiluca miliaris*—Bütschli.

FIG. 12. Diagram illustrating the structure of striped muscle—Melland, Q. J. M. S., xxv. [illegible]

See also 93, *d*—Van Beneden, A. B., iv.—Contraction and amœboid movement accompanied, perhaps caused, by mutual attraction of the microsomata.

FIG. 13. Nuclein filament from a gland-cell of an insect—Carnoy, p. 233.—The chromatic microsomata are arranged in a reticulum imbedded in the surface of the *hyaloplasm filament* (nucleolus).

FIG. 14, *a*. A nucleus of *Amœba proteus*—Gruber, Z. w. Z., xli.—The chromatin granules are largest peripherally. In *b* (Z. w. Z., xl.) there is a differentiation of a large central nucleolus with fine granules from a surface membrane of large, closely united microsomata. At times the microsomata are reduced to so fine granules that only a diffuse staining results.

FIG. 14, *c*. *Chænia teres*—Gruber, Z. w. Z., xl.—The chromatin granules have grown from invisible points.

FIG. 15. *Trachelocerca phœnicopterus*—Gruber, Z. w. Z., xl.—Like Fig. 14, this cell (rhizopod) is multinucleate. In *a* nucleoli appear in each nucleus; in *b* the nuclei have broken down to the state of free microsomata that divide up finer and finer.

FIG. 16. *Haliomma erinaceus*—Bütschli, after Hertwig.—The central capsule only is shown, with its large central nucleus and peripheral smaller nuclei budded from the central one, which has itself peripheral "nucleoli" that resemble the small "nuclei."

FIG. 17. Central capsule of *Acanthometra*. *a*, Bütschli, after Hertwig; *b*, after Stein.—In *b* the nucleoli have become independent bodies, and are separated by irregular division of the nucleus into individual nuclei, probably for reproductive purposes.

FIG. 18. Central capsule of *Collozoum inerme*—Bütschli, after Hertwig, etc. In *a*

the nucleoli are getting clothed with a definitely bounded plasma. In *b* these new cells or germs have become elongate and arranged in a reticulum like that of Hydrodictyon; later they become free and are expelled as flagellate monads, as at *c*. *d* is a young capsule dividing; the nucleus consists of a group of nucleoli (or microsomata.) *e* is an older capsule budding.

FIG. 19, *a–b*. Central capsule of *Thalassicolla pelagica*—Bütschli, after Haeckel. *b* shows the nucleus budding; it now has its chromatin in a filament which here and there preserves its reticulate arrangement seen in *a*.

FIG. 19, *c–e*. Capsule of *Th. nucleata*—Bütschli, from Hertwig, etc.—In *c* the chromatin is in a surface layer of microsomata and a central granular mass. In *d* the microsomata are in the form of beaded filaments. In *e* the capsule contains many small nuclei dividing, and outside are similar groups that have probably migrated from the capsule.

FIG. 20, *a–c*. Nucleus from *Amœba lucida* (multinucleate)—Gruber, Z. w. Z. xli.—The "membrane" bounding the nucleoplasm is at a distance outside of that in which the chromatin bodies lie. These have irregular processes in *a*, indicating the presence of a reticulum. In *c* the nucleus is dividing; the two daughters are still connected by a bridge of hyaloplasm like that which is seen in Figs. 41, 42, etc.

FIG. 21, *a–c*. Nucleus of *A. prima*—Gruber, Z. w. Z., xli.

FIG. 22, *a–d*. Nucleus of *Euglypha alveolata*—Gruber, Z. w. Z., xl.—*a* shows a central nucleolus, *b* many peripheral ones. In *c* they are massed near the centre; in *d* they have multiplied so as to fill the nucleus, and each has taken on itself a structure similar to *a*. This reminds us of the "germinal balls" of Stein and others.

FIG. 23. Nucleus of *Ceratium tripos*—Stein,—filled with germs that are set free to reproduce the mother.

FIG. 24. *Labyrinthula*—Cienkowski, A. m. A., iii. (see Lankester, "Protozoa," Encyc. Brit.).—The plasma in which the simple nucleolus-like bodies live, move, and divide is in the act of digesting a conferva filament.

FIG. 25. A section near the surface of *Sphærozoum neapolitana*—Bütschli, after Haeckel.—A layer of "yellow cells" (symbiotic) lies on the surface. The body is formed of spherical vacuoles, "needles," and a "syncytium" of nucleated plasma masses, united by processes with one another. Compare Fig. 1, also volvox, a reticulum of nerve-cells, and Figs. 8–10, etc. The physiological reason for this structure is probably alike in these various cases. *b* shows a nucleus dividing, the nodes of its reticulum appear as granules. Homogeneous nuclei dividing are often amœboid.

FIG. 26, *a–h*. A nucleus of *Pelomyxa villosa*—Greeff, A. m. A., x.—*a* has one nucleolus. In *c* there are several, one central, and a peripheral set. In *d* each has split up into a group of granules or small microsomata; in *e* these have again united, and in each nucleolus repeats the structure of *a*, and is set free as *g*. *h* is a "refringent corpuscle," formed from *g* by disappearance of the nucleolus.

PLATE II.

FIG. 27, *a–e*. Nucleus of *Klossia octopiana*—Schneider, A. Z. E. G., 2d ser., i.—*a* shows a complex nucleolus budding off smaller nucleoli, which in *c* ultimately become nucleolated; *d* shows nuclei dividing; *e* shows a cyst where the remains of the old nucleus is surrounded by the "spores" that were budded off.

FIG. 28, *a–c*. *Stylorhynchus oblongatus*—Bütschli, after Schneider, A. Z. E. G., iv.—In *a*, a spore-cyst is burst and the spores come out in strings, reminding us of beaded filaments in karyokinesis, also of Figs. 7, 10, *a*, 19, *d*, 31, 41, etc. *b* shows a nucleus budding off spores, and *c* is a spore set free.

Fig. 29, *a–b*. Nucleus of *Carchesium polypinum*—Greeff (see Kent, Plate 50).—The hyaloplasm does not appear constricted between the microsomata as in Fig. 31, etc. Each microsoma behaves like a nucleus and gets nucleoli, which themselves become cells like the germs of the "germ-balls." Sexual conjugation is reported as having preceded this state.

Fig. 30. *a–b*, Nucleus of *Actinobolus radians*—Entz, M. z. S. N., vol. v.—*a*, "germ-ball" state; *b*, stentor state.

Fig. 31, *a–c*. *Stentor polymorphus* (nucleus)—Stein (Kent, Plate 50).—The fork in *a* caused by branched budding of one of the microsomata. In *b* and *c* the chromatin has contracted to form itself into the reproductive state of germs.

Fig. 32. Portion of nucleus of *S. roeselii*—Claparède and Lachmann (Kent).—The nucleolus of the part segmented off becomes the nucleus of a new growth.

Fig. 33. Nucleus of *Urostyla grandis*—Bütschli (Kent).—"Germ-ball" state.

Fig. 34. Nucleus of *Acineta jolii*—Maupas, A. Z. E. G., ser. 1, vol. ix. (Kent).

Fig. 35. Nucleus of *Plagiotoma lumbrici*—Stein (Kent).

Fig. 36. Nucleus of *Oxytricha*—Gruber, Z. w. Z., xli.

Fig. 37. Nucleus of *Chilodon cucullus*—Wrzesniowski, A. m. A. V., vol. v. (Kent).—The nucleolus is nucleated and a "paranucleus" resembling this subnucleolus rests against the nucleus.

Fig. 38. Nucleus of *Acineta fœtida*—Maupas, A. Z. E. G., ser. 1, ix. (Kent).

Fig. 39. Nucleus of *Vorticella*—Gruber, Z. w. Z., xli.—Notice a paranucleus on the concave side of the "horse-shoe" nucleus.

Fig. 40. Nucleus of *Leucophyrs patula*—Kent, Plate 29.

Here are seen two paranuclei.

Fig. 41. Nucleus of *Loxophyllum meleagris*—Bütschli (Kent). Microsomata in act of dividing and so forming the beaded filament.

Fig. 42. Nucleus of *Loxodes rostrum*—Wrzesniowski, Z. w. Z., xx. (Kent).—Paranuclei accompany some of the sub-nuclei.

Fig. 43. Cell from *pedal ganglion of Arion*—Carnoy, p. 212.—The nucleus is in the form of a beaded filament in an "open" knot or tangle ("Knäuel").

Fig. 44. Nucleus of *epidermis* cell of an *Orchid*—Carnoy, p. 215.—The nucleus contains two reticulated nucleoli and a chromatic filament in a "close" tangle. The chromatin is in disks, and the intervening hyaloplasm is not constricted, hence the filament is not beaded.

Fig. 45. Nucleus of *epidermis* cell of *Salamander*—Carnoy, p. 219.—In *a*, a coarse reticulum is formed by fusion of the chromatic filament at various nodes of a close tangle. In *b* the connections have been broken, and a continuous filament once more formed, which, by shortening, becomes an "open" tangle, and the phases of karyokinesis follow. The chromatin is diffused throughout the filament. In *c* we see the chromatin withdrawing from the processes of the meshes and gathering in a definite path to form the beaded filament seen constricted into segments in *d*.

Fig. 46. Longitudinal optic sections of various *chromatic filaments*—Carnoy, p. 232.—To show the disposition of the chromatin. In all the chromatin is superficial, forming a thick wall in *a*, thin in *b*, thick with interior processes in *c*, and in *d* all gathered in annular segments distinct from one another.

Fig. 47. A filament dragged out of the nucleus by the section-knife, Carnoy, p. 234, shows that the chromatin is sometimes arranged in a spiral on the wall of the hyaloplastic filament, and may be pulled out like the threads from spiral ducts of plants.

Fig. 48. Fragment of a branching *Acinetan*—Bolton (Kent, Plate 47).—The nu-

cleus runs like an axis through all the stems and branches, and is segmented off into all the buds and spores.

FIG. 49, *a–h. Amphibian pancreas cell*—Ogata, A. A. P. (Phys. Abth.) 1883.—The tissue hardened in warm corrosive sublimate is cut into thin sections and stained successively with *hæmatoxylin*, *nigrosin*, *eosin*, and *safranin*. Gaule, the author of this method, claims that there are two substances in the *cytoplasm*, one *eosinophilous*, the other *nigrosinophilous*. There are also two substances in the *nucleoplasm*, one staining best with *hæmatoxylin* (ordinary *chromatin*), and the other best with *safranin*. The *chromatin* is represented dead-black or heavily reticulated, the *safraninophil* is outlined only; the *eosinophil* is marked with parallel lines, the *nigrosinophil* by crossed lines and dots.

a. The nucleus lies imbedded in cytohyaloplasm (nigrosinophil) well marked on one side. On the other are the *zymogen granules* (eosinophil). A sparse reticulum, several small and mostly peripheral nucleoli (chromatin), and one large nucleolus, the "plasmosoma" (safraninophil), occupy the nucleus. In *b* the plasmosoma is migrating from the nucleus which now atrophies. In *c* the plasmosoma, now in the cytoplasm, begins to develop the two constituents of cytoplasm in its interior. It grows rapidly (*d*) to the size of the old nucleus, alongside which it lies. In *e* it has become still larger, and most of it has become transformed into zymogen granules and cytoplasm. In the centre of the remainder, *f*, a chromatin nucleus appears, which, later, differentiates in its interior, the plasmosoma and other nucleoli, *g*, *h*; and so we are back to stage *a* again.

FIG. 50. Nucleus of egg of *Colymbetes fuscus* (Will, Z. w. Z., xliii.), during ovigenesis and yelk formation.—*a*, reticulated; *b*, nucleolated; *c*, the chromatin growing and enlarging one or more of the nucleoli until all is homogeneous in *d*. It then buds off large and small cells; the former become reticulated and atrophy, the latter become follicle-cells. Then sheet after sheet of the nucleus dissolves off and is transformed to yelk-granules (*e*, *f*, *g*), the chromatin breaks down into granules, and microsomata of a beaded filament in a reticulum enclosing several nucleoli (*h*, *j*), and finally the karyokinetic spindle of the polar globule is formed.

FIG. 51. Nucleus of egg of *Ascaris megalocephala*—*b*, *c*, Van Beneden, A. B., iv.; *a*, Nussbaum, A. m. A., xxiii.—The multiplication of a single nucleolus produces one large nucleolated nucleolus (the "prothyalosome") and several smaller ones; *b*, the prothyalosome alone takes part in forming the polar globules, and its residue copulates with the male pronucleus; *c* is the nucleolus of the prothyalsome highly magnified, seen to consist in this stage of two disks, each of four-beaded filaments (the beads being the chromatic microsomata). Compare Carnoy, see Fig. 124.

FIG. 52, *a–c*. Nucleus of egg of *Pike*—Carnoy, p. 233.—In *a* we have a reticulum and nucleoli. In *b* the reticulum is broken up into nucleoli. In *c* these have fused to three.

FIG. 53. Nucleus of egg of *Nephthys scolopendroides*—Carnoy, p. 237.

FIG. 54, *a–b*. Nucleus of egg of *Field-Mouse*—Rauber. M. J., viii.

FIG. 55, *a–b*. Nucleus of egg of *Perch*—Rauber. M. J, viii.—In *a* the microsomata are superficial and their processes suggest a reticulum; *b* is an optic section.

PLATE III.

FIG. 56, *a–f*. Nucleus of egg of *Arion* during ovigenesis and yelk formation, Platner, A. m. A., xxvi.—In *a* we see a nucleolus and microsomata and a paranucleus. In *b* the membrane of the nucleus shows the presence of a sparse reticulum, but the microsomata have concentrated to form a reticulated nucleolus, while the old nucle-

olus is left outside as a paranucleolus. In *c* the nucleolus is homogeneous. In *d* it has microsomata, which fuse to one "nucleolus-nucleus" in *e*. Finally, in *f* the nucleolus has all the structure of the old nucleus of stage *a*. The membrane of the old nucleus now dissolves in the yelk, leaving the paranucleus as a "yelk nucleus."

FIG. 57. Nucleus of egg of *Toxopneustes*—Flemming.

FIG. 58, *a–j*. Nucleus of egg of *Spider*—Carus, Z. w. Z., ii.—In *b* a paranucleus appears, whose changes are as complex as those of the nucleolus. Finally, in *j* we have only a vesicle left.

FIG. 59, *a–f*. Nucleus of egg of larva of *Libelula*—Valette St. George, A. m. A., ii.—The structure of the large nucleolus in *c* reminds us of the entire nucleus of Fig. 51, *b*.

FIG. 60, *a–f*. Nucleus of egg of *Asteracanthion*—Van Beneden, Q. J. M. S., xvi.—The vesicle stage of *f* is reported finally to disappear.

FIG. 61, *a–f*. Nucleus of egg of *Rabbit*.

FIG. 62, *a–b*. Nucleus of *Gonothyraca loveni*—Bergh, M. J., v.—Multiplication of nucleoli by division.

FIG. 63, *a–e*. Nucleus of egg of *Bat*—Beneden and Julin, A. B., i.

FIG. 64. Nucleus of egg of *Anodon*—Flemming, A. m. A., x.—A paranucleus is seen also.

FIG. 65, *a–b*. Nuclei of sexual cells ("primitive ova") of *Rana*—Nussbaum, A. m. A., xviii.—*a* of male, *b* of female. Budding of the nucleus in ovigenesis and spermatogenesis at this stage is often reported.

FIGS. 66–93 illustrate the formation of the spermatozoon from the nucleus of the "spermatid," and points in its structure.

FIG. 66. Antherozoids of *Hymenophyllum*—Carnoy, p. 226.—*a* shows the large reticulate nucleus of the daughter-cell of an antheridium. In *b* the nuclei are elongating, curved, and at its smaller end the net-work of chromatin is changing to the diffuse state. In *d* the pointed end protrudes from the cell and bears the locomotive cilia. This is homologous with the head end of a spermatozoon. The cytoplasm is gradually utilized as pabulum by the antherozoid, the residue remaining stuck to its hinder end *e* (which is finished last), to be finally fully absorbed or thrown off as at *f*.

FIG. 67. Spermatozoid of *Anodonta cellensis*—Carnoy, p. 225.

FIG. 68. Early stage of spermatozoid of *Salamander*—Flemming.

FIG. 69, *a–b*. *Human spermatozoa*, not yet freed from their matrix—Wiedersperg, A. m. A., xxv.

FIG. 70. Spermatozoid of *Elephant*—Weidersperg, A. m. A., xxv.—The head and tail project from the cell, the "neck" or "middle" piece is still growing. In the cytoplasm are the remains of the paranucleus.

FIG. 71, *a–e*. Spermatogenesis of *Rat*—Brown, Q. J. M. S., July, 1885.—*a*, nucleus of spermatid beginning its transformation. At one end the chromatin becomes diffuse, and here also is a *head-corpuscle*. At the opposite end is a *tail-corpuscle*. In the cytoplasm lies a paranucleus. *b* shows the fine *axis of the neck and tail* proceeding from near the *tail-corpuscle*. In *c* the whole nucleus has become homogeneous, elongated and curved, and mostly protruded from the cytoplasm. *d* shows the sperm. nearly completed, a relic of cytoplasm remains sticking where the head and neck join, and another where the tail and neck join. The latter contains the remains of the paranucleus ("seminal granules"). *e* is the completed sperm. The neck shows a spiral structure.

FIG. 72, *a–f*. Sperm. of *Bull*—Kölliker, Z. w. Z., vii.; *g–k*, Brunn, A. m. A.,

xii. and xxiii.—The multiplication of the nucleus of the spermatogonium when the division of the cytoplasm is partially or wholly suppressed, causes several spermatids (and hence spermatozoa) to be united to or in a single cell, and so forming spermatogemmes. *a–d* illustrate this point, which with mammals is not the rule. The concentration of chromatin in one side of the nucleus near a head-corpuscle, the formation of a cap in connection with this corpuscle, is illustrated in *g–k*. The other granule is either the paranucleus or tail-corpuscle. In *k* the membrane covering the middle and hinder part of the head is lost or not separated away like the cap. The "collar" about the neck is the membrane of the old cell.

FIG. 73, *a–f*. Sperm. of *Rabbit*—Brunn, A. m. A., xii.—*a*, after Platner, A. m. A., xxv., shows the paranucleus, the cap and head-corpuscle, the chromatic head enveloping the forward end of the neck-piece or its axis. *b* shows the nucleus in two parts, the posterior portion grows smaller, the chromatin is concentrated in the anterior part of the anterior portion, which forms the head. *e* is from Schweigger-Seidel, A. m. A., i., to show the finished spermatozoon.

FIG. 74. Sperm. of *Mouse*—Brunn, A. m. A., xxiii.—Corpuscles arrange themselves about the axis of the middle piece and build it up, so that in the finished specimen the neck is annulated.

FIG. 75, *a–c*. Sperm. of *Sparrow*—Brunn, A. m. A., xxiii.—Here the cytoplasm spins a filament that winds spirally about the axis, but remains separate from it.

FIG. 76, *a, b*. Sperm. of *Pigeon*—Kölliker, Z. w. Z., vii.

FIG. 77. Sperm. of *Triton*—Schweigger-Seidel, A. m. A., i.—The sinuous filament represents the thickened edge of a delicate membrane, which slings it to the tail like a mesentery. See Gibbes, Q. J. M. S., xix., for same structure in salamander, and Fig. 78, *c–e*, for the frog.

FIG. 78, *a–e*. Sperm. of *Bombinator*—Valette St. George, A. m. A., xxv.—*e* is the skeleton left after macerating away the sarcode.

FIG. 79, *a–e*. Sperm. of *Raja clavata*—Jensen, A. B., iv.

PLATE IV.

FIG. 80, *a–e*. Sperm. of *Branchiobdella*—Voigt, A. z. z. I. W., vii.—In *a* we have a large nucleus, to which is fastened a *tail-corpuscle;* we have also a small paranucleus, but this grows, fastens itself to the nucleus at the end opposite the *tail-corpuscle*, and proceeds to spin a spirallated piece like the middle piece of Figs. 71, 79, etc., but it here has the place of a head-cap, though its functions are probably unchanged.

FIG. 81, *a–f*. Sperm. of *Helix*—Platner, A. m. A., xxv.—Here the nucleus buds off a paranucleus, then concentrates, becomes homogeneous, an axis appears, over its end the nucleus invaginates itself, while the cytoplasm containing the paranucleus spins three spiral filaments; two of these closely invest the axis, the third remains free.

FIG. 82, *a–c*. Sperm. of *Cassiopeia*—Mereschkowski, A. Z. E. G., x.—In *c* the dotted line is a portion of the circumference of the "blastophore," the protoplasmic "cell" which bears the spermatozooids imbedded by their heads over its surface.

FIG. 83, *a–e*. Sperm. of *Cucumaria frondosa*—Jensen, A. B., iv.—Head- and tail-corpuscles are seen. In *e* a middle piece in connection with the tail-corpuscle is seen. The spermatozoon is still unfinished.

FIG. 84, *a–g*. Spermatazoon of *Paludina vivipara*—"hair form" (functional), Brunn, A. m. A., xxiii.—In *b* are seen two tail-corpuscles and peripheral microsomata of chromatin that diffuse in *c*. *f* is the finished sperm., *g* is a bundle of them.

FIG. 85, *a–f*. Sperm. of *Paludina vivipara*—vermiform (not functional), *a–e*, Carnoy, p. 228.—The nucleus here plays no direct part in the formation, but acts like a paranucleus. *d–f*, Brunn, A. m. A., xxiii. The nucleus is here represented as directly concerned. Compare *f* and 84, *g*.

FIG. 86, *a–j*. Sperm. of *Locusta viridissimi—a*, *b*, and *h*, Valette St. George, A. m. A., x.; *c–j*, Brunn, A. m. A., xxiii.—Here, as in Fig. 73, the head (*f*) divides into two parts, the anterior of which contains the chromatin.

FIG. 87, *a*, *b*. Sperm. of *Forficula auricularia*—Valette, A. m. A., x.

FIG. 88, *a–d*. Sperm. of *Stenobothrus*—Valette, A. m. A., x.—The middle piece (at least its periaxial portion) is formed directly from the paranucleus.

FIG. 89, *a–g*. Sperm. of *Blatta germanica*—Valette, A. m. A., xxvii.—The paranucleus is reported as formed from a granular mass, and it evidently is built into the "middle piece." In *e* and *g* globules of cytoplasma are seen sticking to the flagellum (neck [middle piece] and tail).

FIG. 90, *a*, *b*. Sperm. of *Agrion*—Bütschli, Z. w. Z., xxi., pp. 402 and 536. *c*, *Hydrophilus*. (*Clausilia*, *Aeridia*, *Clythra*, etc., agree closely with Figs. 87, 88, 89, 90.)

FIG. 91, *a–j*. Sperm. of *Astacus—a–g*, Grobben, A. z. I. U. W., i.; *f*, *h*, *j*, Nussbaum, A. m. A., xxiii. *j* is view from above.

FIG. 92, *a–e*. Sperm. of *Eupagurus*—Grobben, A. z. I. U. W., i.

FIG. 93, *a–d*. Sperm. of *Ascaris megalocephala*—Van Beneden, A. B., iv.—*a*, Spermatocytes forming from the spermatogonium. The two nuclei are united by the *spindle*. In *b* spermatids have formed, held together in a spermatogemme by a "cytophoral" portion (in which is a "*refringent body*" connected with each spermatid, homologous with paranucleus). *c*, the mature sperm. The nucleus is situated in the head, which is left uncovered by the thin membrane that covers the remainder. The "refringent body" is large, and fills up nearly the entire body. *d*. Here the refringent body is small, the protoplasm about the nucleus in the head, amœboid. The microsomata of the cytohyaloplasm, seen in rows, mark the nodes of a regular reticulum.

FIGS. 1–13, 25, 66–68, 71, 81, 93, illustrate the *structure of protoplasm*.

FIGS. 1, 2, 6, 16–18, 22–34, 49, 59, 66, etc., illustrate the "*individuality*" *of the nucleus* or of its subordinate parts.

FIGS. 13, 14, 17, 19, 20, 28–51, illustrate the different *forms of nuclei*.

FIGS. 8–10, 13–15, 19, 20, 26, 28, 43–47, 49–61, illustrate the *different conditions and morphological structure* the nuclein may assume aside from the changes of *karyokinesis*. Still other examples will appear when *karyokinesis* is considered.

FIGS. 50–64 (exc. 62) illustrate the *structure of the* "*germinal vesicle*."

FIGS. 66–93 illustrate the *structure of the spermatozoon*. (Only a small piece of the tail has in each case been represented, to economize space.)

FIGS. 36–40, 42, (44?), (49!), (50?), 56, 58, 64, 70, 73, 78, 80, 81, (83?), 84, 86–93, indicate the presence of a *paranucleus*. Other cases will be given under *karyokinesis* and *fertilization*.

EXPLANATION OF PLATES V.—VIII.

Figs. 94 to 124, *h*, illustrate cell-division (94–104 are Protozoan), and Figs. 124, *j*,–133 illustrate fertilization (*i.e.*, the union of male and female pronuclei).

PLATE V.

FIG. 94. *a–b. Opalina ranarum*—Kent, Plate 26. See also Nussbaum, A. m. A., xxvi., and Zeller, Z. w. Z., xxix.—This "unicellular" animal is multinucleate, and the nuclei multiply by karyokinesis (see Figs. 104, 105) independently of cell-division. The latter takes place successively as in *a*, until small cells like *b* result, containing few nuclei. These become encysted and the nuclei fuse to become one. Then the mononucleate animal escapes and increases in size, while the nuclei become more numerous again. Their number may rise to hundreds.

FIG. 95, *a–d. Oxytricha scutellum*—Gruber, Z. w. Z., xl.—As this infusorian grows the number of nuclei increases by direct division until we have a form like *c*, then the nuclei fuse (*d*) to become one, and then once more divide. As this proceeds the cell-body is constricted between the groups of nuclei as shown in *a* and *b*.

FIG. 96, *a–b. Polyerieus schwartzii*—Bütschli, A. m. A., ix.—This infusorian usually has a row of four nuclei as in *a*, but when division takes place the nuclei divide so as to furnish the daughters with the normal number (*b*).

FIG. 97, *a–d. Stylonychia histrio*—Nussbaum, A. m. A., xxvi.—Here we have two sorts of nuclei, a small spindle-shaped "paranucleus," which in division presents the spindle-fibres and microsomata of karyokinesis, and a large nucleus whose "nuclein" substance is more irregularly distributed. In a resting state (*a*) the paranucleus is homogeneous and nearly spherical, the nucleus has small bodies in it that resemble the paranucleus. When cell-division takes place (*b*, *c*) both sorts of nuclei divide so that the daughter cells are multinucleate, but when these return to the "resting" condition the nuclei fuse once more, as seen in *d*. Here the nuclein bodies of the nucleus are drawn out into filaments.

FIG. 97½, *a–b*. Represents division of *Paramœcium*,—from article "Protozoa" in Encyclopæd. Brit., by Lankester. Here the paranucleus divides into two groups of four each, but the nucleus divides up much finer and strongly suggests beaded filaments. Bütschli in A. m. A., ix., figures the nucleus as broken up more irregularly.

FIG. 98, *a–g*. *Polytoma uvella* (*a–e*, *f–g*) and *Dallingeria drysdali* (*d* and *e*) —Dallinger, Jour. R. Micr. Soc., April, 1886.—After conjugation (see Fig. 131) the fertilized nucleus of the monad is dissolved throughout the protoplasm in ultra microscopic particles (gemmules), and when the cyst bursts these are projected out, and soon grow so as to be visible to a power of fifteen thousand diameters, until finally they attain the size and shape seen in *a*, then granules appear in their substance, and at the same time a clear zone of protoplasm (*b*) is secreted about this body, which henceforth is the nucleus (*c*). When division is to take place the granules arrange themselves in regular lines as in *d*, and a peculiar and simple karyokinesis follows (*e–f*), with return of granules to normal distribution in *g*, a daughter-nucleus.

FIG. 99, *a–c*. Nucleus of *Chromulina woroniana*—Fisch, Z. w. Z., xlii.—The wall of the nucleus is thick and contains nuclein, but there is also a nucleolus which segments up into fine granules, while simple constriction of the nucleus ensues (*a–c*), and when the daughter-nuclei are established, these granules fuse and return by inverse kinesis to the normal state.

FIG. 100, *a–d*. Nucleus of *Cyathomonas truncata*—Fisch, l. c.—This is thin-walled, and most all the chromatin is in the nucleoli. In *a* four of these bodies are

seen. In *b* we see rows of granules raying out from the nucleolus, and the nucleus and nucleolus behave in division much as if the former were a cell and the latter its nucleus; finally, after division (*c–d*), the rays disappear, and we get a simple nucleus with a nucleolus.

FIG. 101, *a–e*. Nucleus of *Cordosiga botrytis*—Fisch, l. c.—We have first a clear vesicle containing a nucleolus, the latter gradually dissolves into granules (*a*, *b*), and the granules fuse to filaments (*d*), which arrange themselves parallel to one another like a spindle, and then the fibre-bundle constricts, followed by the nucleus (*e*). The original state is assumed by the daughter-nuclei passing through an inverse series of changes: thus from *e* we get successively *d*, *c*, *b*, *a*, etc.

FIG. 102, *a–b*. *Onychodactylus acrobates*—Entz, Mitt. Neap., v.; *c*, *Stylonychia mytilus*—Bütschli (from Kent, Plate 1.).—Division of nucleus and paranucleus during cell-multiplication. The nucleus and paranucleus remain closely applied to each other; the latter *leads* in division. The segments of the former remain united by a bridge (*c*), the centre one only being severed by cell-division as in *b*.

FIG. 103, *a–g*:—*a–c* Nucleus of *Spirochona gemmipara*—Hertwig, Jenaische Zeitschrift, xi. *d–q* is a nucleus of *Actinosphærium eichornii*—Hertwig, Z. z., xviii.; see Gruber, Z w. Z., xxxviii.—*a–c* show the amœboid powers of nuclear substance; in *a* the phenomena are restricted to the nucleus; in *b* to the hyaline body which holds the nucleolus, and at last, in *c*, the nucleolus is sending out ray-like pseudopodia, which become the chromatin fibrils. A spindle is finally formed with a hyaline end-plate at each end. *d–h* show different states of a nucleus in the "resting" condition. In *d* we have a nucleolus and paranucleolus; these segment and become related, as in *e* and *f*. In *g* the nucleolus is much segmented. *h* shows us the nucleus preparing for division; the special protoplasm sheet lining the nucleus is amœboid, as is also the nucleolus. The former, at last, gathers as two polar caps (*j*), while the latter dissolves to granules (*k*); at first the granules are in the centre of the nucleus, then they pervade its whole substance, and finally a peripheral clear zone is established (*k*). The substance of this zone then moves to the poles, forming a "polar plate," while the granules aggregate in vertical lines, and fuse more and more towards the equator to form an equatorial plate of microsomata (*l*). Then segmentation begins again, and the daughter-microsomata move apart towards the poles (*m*). On their way they form a continuous plate or zone of very minute granules (*n*), but sometimes the groups may be shown to be still distinct, as at *o*, which also shows the polar *stars* ("asters") raying out from the protoplasmic cap. The microsomata are received and absorbed by the polar plate in a rosette-like figure (*p*). The polar plate invaginates like a gastrula, while the spindle constricts; the polar masses of protoplasm flow down on the sides (*q*), and are at last themselves constricted to serve as an envelope for the daughter-nuclei; the spindle-fibres are absorbed into the cavity of the gastrula-like "calotte," and a stage-like *h* results. The substance of these fibrils is probably that which is separated from the nucleolus to form the paranucleolus.

FIG. 104, *a–c*. A nucleus of *Opalina ranarum*—Nussbaum, A. m. A., xxvi.—The nucleus divides by first forming four "microsomata nucleoli," seen in polar view in *a*. These microsomata divide and move along fibres to the poles, as in *b*, and simple constriction, as in *c*, and reversion to uninuclear condition follows.

105, *a–j*. A nucleus of *Opalina ranarum*. According to Pfitzner (M. J., xi.), *a* shows an irregular reticulum or "knäuel" with a couple of nucleoli and irregular masses of chromatin at the surface. In *b* the chromatin has become aggregated in superficial microsomata. These are forms of resting nuclei. The initial condition

from which division proceeds is seen in *c*. We have an abundant knäuel and a few nucleoli; then in *d* the knäuel (skein) filament segments; next, in *e*, the segments are concentrated to the centre. The nucleoli may or may not be absorbed. Now there ray out fibres from an "amphiaster" towards the centre from two opposite points, and the segments of nuclein arrange themselves into an equatorial plate (*f*), and, splitting each into two, send the regular number of V-shaped loops along the fibres of the spindle to the poles (*g*, *h*). Constriction follows (*j*), and the segments once more fuse into a "skein-filament" or a "reticulum." This gives us as complicated a form of karyokinesis as we find in the cells of metazoa.

FIG. 106, *a–d*. Nucleus of embryonic cells of *Scorpion*—Blochmann, M. J., x.—To show "direct" division. A nucleolus is built up from *a* to *b*; the nucleolus then divides, next the nucleus does so, and at last the cell constricts according to the Remakian scheme.

FIG. 107. Nucleus of *Vorticella* in division—Carnoy, p. 217.—Shows a simple constriction without modification of the net-work.

FIG. 108. Epithelium nucleus from gut of *Astacus*—Frenzel, Mitt. Neap., v.—No karyokinesis during division, though we have a reticulum and nucleoli.

FIG. 109. Male ovum of *Pelobates fuscus*—Carnoy, p. 40.—Cell and nucleus suffer simple constriction; the segments of the nucleolus are thus separated without a spindle,—a mode of division known as "stenosis."

FIG. 110. Nucleus of muscle-fibre of larva of *Hydrophilus* (Carnoy, p. 240) entering into division. The segments of the nuclein filament are seen lying among the fibres of the spindle, which latter have been transformed from the karyoplasmic net-work.

PLATE VI.

FIG. 111, *a–k*. Nucleus from cells of endoderm of Cœlenterates except (*k*) which is ectodermal—Pfitzner, A. m. A., xxii.—*a* gives the "skein" reticulum; *b* shows the skein-filament segmented, while the nucleolus has divided. In *c* we get the segments in centre; in *d* the nucleoli have dissolved; in *e* the polar asters have formed a spindle, and the segments have formed a "rosette" in its equator; *f* shows the "rosette" broken up into loops by segmentation of outer limbs of the rosette. This is the "monaster" stage, and when the loops have split and duplicated themselves we get in *g* the "dyaster." *h* shows the spindle with the loops near the poles and with astral rays streaming out into the cytoplasm; *j* shows the constriction of spindle and of cell; in *k* we have a true skein-filament that does not form a reticulum.

The formation of the cell "plate," where (as in plants) there is no cell constriction, may be seen in Figs. 124, *h* and *s*, and modern text-books on botany.

FIG. 112, *a–g*. Karyokinesis from epithelium of *Salamander*—Flemming, A. m. A., xviii.—*c*, *d* are from testes as seen in living state. Here we see bodies at the poles nearly corresponding in number to the segments of the filament. When the dyaster is formed they are about twice as numerous, and strongly suggest that they are a species of paranucleolus. *cf.* 97½, 103, etc. In the daughter-nuclei the series *a*, *b*, is inversely followed, as in *e*, *f*, *g*. In *g* the filament is cut across by the knife in many of its windings, thus giving us pseudo-nucleoli.

FIG. 113, *a–g*. Epithelium of *Salamander* according to Rabl, M. J., x.—*a* is a schematic side view, and *b* a polar view of a resting nucleus. According to Rabl the segments of the filament do not fuse or in any way anastomose in the resting nucleus, but simply branch out finer and finer. Then in kinesis the branches are withdrawn, and short thickish loops are formed. The spindle is first seen in its entirety at one pole, which, as seen in *a* and *b*, is different from the other pole, and then the spindle

turns at an angle of 90° and forms the usual amphiaster (*c*, *d*). When the loops split, the halves are carried apart at their *bend* first, and the shorter arms of the U are first separated as seen in *e*. Arriving at the poles the loops branch out once more, as in *f*, to form the figure *a*. In *g* we see a daughter-nucleus from testicular epithelium of Proteus, where the branching does not take place, but the loops are formed of a row of microsomata (beaded filament).

FIG. 114, *a–b*, shows how such a beaded filament splits by each microsoma dividing in the general plane of the loop. Pfitzner, M. J., vii.

FIG 115, *a–e*. Nucleus from growing point of *Tradescantia virginica*—Strasburger, "Zellbildung u. Zelltheilung," Jena, 1880.—The nearly homogeneous protoplasm of the nucleus (*a*) becomes granular; the granules fuse and arrange themselves in rows of microsomata (*b*), and these rows are cut across (*c*) in the equator and pushed towards the poles while undergoing various changes of segmentation back to granules again, but a central nucleolus remains undissolved, or rather is built up during the process of reconstruction of the daughter-nucleus (*d*, *e*).

FIG. 116, *a–e*. Nucleus of *Spirogyra majuscula*—Strasburger, l. c.—In *a* we see the lenticular nucleus with its nucleolus; *b* is a face view showing it becoming granular. In *c* the nuclein has segmented (or aggregated?) into more and more numerous masses or microsomata which soon reach the granular state again (*c*, *d*, *e*). Meanwhile the nucleus flattens more and becomes biconcave; the granular protoplasm gathers in the concavities and sends across and through the nucleus the spindle fibres (*e*); the marked boundary of the nucleus is dissolved, and the equatorial plate of granules splits and moves towards and into the polar masses, while the intervening portions of the spindle-fibres ("connecting fibrils") spread out and help build the cell plate.

FIG. 117 is from *Spirogyra nitida*, where the nucleus is more spherical and the spindle-fibres are at first aggregated towards the centre in union with the central granular mass of chromatin, and they become more spread out as the nucleus loses in outline and the chromatin is divided into its daughter portions. We see also that the latter is confined to the central fibres of the spindle.

FIG. 118, *a–dz*. Nuclei from protoplasmic layer next wall of embryo-sac of *Galanthus nivalis*—Strasburger, A. m. A., xxiii.—*a*, first step towards karyokinesis; the microsomata form a continuous beaded filament, produced by the shortening of a finely-wound "skein" or "tangle," the meshes of whose reticulum give a finely granular appearance to the protoplasm. A large nucleolus exists besides. This is dissolving and adding itself to the filament in *b*, where the boundaries between the microsomata are not indicated in the diagram. *c* is the "segmented stage," in which we have on both sides of the equator segments whose equatorial ends are bending around like hooks (only a few segments are shown). Next, the hooks split longitudinally, and the halves of each hook seek opposite poles; to do this there must be a stage where one-half of the loops of the southern hemisphere cross the equator and meet corresponding hooks from the northern on their way to the southern hemisphere. (See *d*, where *w* and *w'* are the corresponding halves of the southern hooks, and *x* and *x'* of the northern hooks. *w'* and *x'* are represented as having just crossed.) While this "metakinesis" is progressing the hooks become more U-shaped, and taking the northern daughter-nucleus, as in *dy*, we can see how its skein-filament is reconstituted in *dz*, by union of neighboring limbs of the sets of loops. (Metakinesis refers to the changes that take place after the splitting of the loops or microsomata to form the chromatin figures which are to occupy the daughter-nuclei. The preceding changes constitute the "prophase," the succeeding, the "anaphase.")

FIG. 119, *a–l*. From wall of embryo-sac of *Fritillaria imperialis*—Strasburger,

A. m. A., xxiii.—*a–d* represent the prophase, *e–f*, the metaphase, *g–l*, the anaphase. Here the first step of the metaphase is, as in the last case, one of mutual transfer between the opposite sides of the equator. (See *f*.) Following any one loop in the northern hemisphere, splitting into two halves (1, 2, Fig. *fw*), the part 2 is destined for the northern daughter-nucleus, and 1 for the southern. Separation between the two halves proceeds from one end to the other, so that the part 1 becomes pulled out straight, one limb of the part 2 is held back, while the other is dragged towards its own pole (*fx*), both halves are therefore acted on so as to be pulled into line parallel with a meridian, but the end, as it approaches the pole, bends around hook-shaped to form a new loop, hence the part 2 passes through an "S" stage (*fy*), and the part 1 a hook stage, and they finally reach the U stage in *fz*, when the stages *dy* and *dz* ensue, as in the preceding figure. On comparing Figs. *f–l*, it will be seen that practically this mathematical regularity is never attained, but only distantly approximated. The number of loops in Strasburger's figures is far greater than in the diagram, but they may be deciphered and understood by means of the diagrams (Fig *f–fz*). The main source of departure is found in the fact that most of the loops are not perfect U's in the anaphase, but are oftener hooks or even straight filaments lying in the meridians. In the last case *fw* and *fx* would be omitted.

FIG. 120. Cell from testis of *Chelonia caja*—Carnoy, p. 250.—The nuclear spindle is nearly constricted off in the equator; the cytoplasm is partly so, and shows its fibres as regularly arranged as those of the spindle.

FIG. 121. Dividing sperm-cells from *Rat*—Weidersperg, A. m. A., xxv.—The two cells are at a distance from each other, but still the spindle-fibres unite the two daughter-nuclei.

PLATE VII.

FIG. 122, *a–t*. From pollen mother-cells of *Fritillaria persica*—Strasburger, A. m. A., xxiii.—*a–g* is the prophase, *h–m* the anaphase, *m–r* a succeeding prophase, and *r–t* the next anaphase. The filament is at first much finer and more intricately woven than represented in the first three diagrams. In *b* we see a nucleolus at one pole in connection with which the loops of the skein are put; *c* is a polar view of the same. In *d* the filament has shortened more and passed out of its relation with the polar nucleolus, which is now breaking down. Next, in *e*, the segmentation is completed, and the limbs of the U shaped segments are closely applied to each other; then, in *f*, these stumpy "loops" get crowded into the centre, and the spindle is formed (*g*). Then splitting ensues and metakinesis (*h*). In the daughter-nuclei the loops come to lie so as to make the poles of the nucleus unlike: side view in *j* and *k* and polar view in *l*, where the open ends of the loops point towards the old equator. Finally the daughter-nucleus is constituted as in *m* and *n* side and surface (polar) views respectively. But as it is about to divide again, the return to the resting state is not complete, immediately a continuous filament is established, with local thickenings on it, showing the chromatin already segmenting. While segmentation proceeds, the segments get into the meridians and shorten towards the equator (*p* and *q*), then the spindle is formed (*r*), and after the anaphase straight rods of chromatin pass to the poles, where they curve into loops (*s*, *t*). This series shows what variability there may be between successive divisions of same nucleus. Such variability has also been reported by the next (Fig. 123) and Carnoy (Fig. 124).

FIG. 123, *a–qx*. Spermatogenesis of *Helix pomatia*.—*a*, the nucleus, with a thin layer of protoplasm about it, forming the "sperm mother-cell." It is now homogeneous, soon becomes granular, and a reticulum is developed (*b*). Out of the nucleus now buds a paranucleus (*x*). Then there is a period of growth until we get *c*, with

a rich surface reticulum of chromatin. In *d* the meshes of the reticulum have been absorbed by the karyosomata. In *e* each karyosoma has by binary segmentation formed four microsomata; these re-establish the net-work by separating to equidistant distribution, and, by retracting the connecting processes in some directions and strengthening them in a meridional direction, they form a series of loops of a filament (*f*). The paranucleus now approaches the pole, and at the same time the loops contract towards it, forming a rosette (*g*). The outer turns of the rosette break, as seen in polar view given in *h*. The paranucleus is absorbed, and the loops with their bends towards the axis move down to the equator (*j*); at the same time the spindle is formed. Here each loop shortens into a single karyosoma, forming fourteen to twenty such bodies in an "equatorial plate (*k*); the fibres of the spindle are in union, by means of the rays of the polar aster, with the cytoplasmic reticulum. Each karysoma now segments again into four microsomata (*l*), but only the first plane passed in the meridian cuts through completely; the second is simply the beginning of an attempt to form a beaded filament. These short filaments, consisting each of a pair of microsomata, now pass through the metaphase; but on their way the microsomata fuse to form the karyosomata of the daughter-nuclei (*m*, *n*). The spindle-fibres are utilized in forming the paranucleus (see A. m. A., xxvi.), the karyosomata segment to form the rosette *p* and *px*, where *p* is the figure in the first division and *px* that of the last. The reticulum is again established in *q* and *qx*; the steps following the final division are shown in Fig. 81, *a*, *b*, *c*, etc.

FIG. 124, *a–s*. "Cytodieresis" of the egg of *Ascaris megalocephala* (*a–g*), from Carnoy—La Cellule, vol. ii., May, 1886. *h–s* from Van Beneden, A. B., iv.—*a* is the nucleus of a young egg having a beaded filament forming a "skein." There is besides a nucleolus which Carnoy calls a "plasmatic-nucleolus" (*x*). Soon the filament segments (*b*) into eight karyosomata, and then the reticulum of the nucleus can be seen remaining. The egg grows, and when mature, and containing the spermatozoon, the preparations for forming the polar globules are made. The poles of the egg become marked each by a plasmatic-nucleolus; and the eight karyosomata now take an equatorial position in two groups (*c*), which gives to the germinal vesicle the appearance of having two germinal spots when viewed with moderate powers. The next stage shows the reticulum and wall of the germinal vesicle dissolved (which solution appears with all nuclei at this stage). Two groups of fibres now ray down from one pole towards the karyosomata (*d*). The other half of the spindle is soon completed in a similar manner. Then from the poles, where is a granular mass called a "plateau," there ray out into the protoplasm, fibres to form primary asters (1). The plateaux may split and so form several secondary plateaux, one of which is shown at 1′, Fig. *e*, for each pole, but its aster is still primary, because a part of its rays enter into the nuclear spindle. There may be several of these formed by repeated splitting of the "plateau." Secondary asters (2) are formed when the streamers flow from the karyosomata. Tertiary asters (3) are those connected with primary asters, but not a part of nuclear spindle; while quatenary asters (4) are small asters scattered through the yelk, but they may be connected with any other aster by one or two filaments. These asters are simply transformation of the ordinary reticulum, and no fixed law governs their production, and the utmost variety of combination may be found. The system of asters is much more complex in the formation of the second polar globule than in the first. Our description of Fig. *e* is from the second "caryocinetique figure." The asters finally fade out until only one plateau with its bilateral spindle is left; this often closes up on itself (*f*), so that the polar plate looks like an equatorial plate; the karyosomata are thus carried around into a plane at right

angles to their old position, and tend to approach each other. But this mode of disappearance of the asters is only one of several. The last trace of the spindles and asters disappears (*g*), the plateaux are reduced to granular spots, the reticulum of the plasma is restored, but not as yet the membrane of the nucleus. Now the reticulum produces a simple spindle anew (the "spindle of separation") between the two groups of karyosomata, and the most peripheral one is cut off by an equatorial cell plate, much as in plants (*h*). The segment cut off, which sometimes contains part of the yelk, is the polar globule. Then the four karyosomata of the yelk separate into groups of two each, and the process is elaborately repeated, so that only two karyosomata are left in the yelk to form the female pronucleus. The karyosomata in the polar globules may divide by karyokinesis. After the last polar globule has been extruded (*h*) the two karyosomata of the female pronucleus segment up into microsomata, and a similar figure is seen with the nuclein of the male pronucleus. *j* shows the two in a stage where a beaded filament is being established by concentration and shortening; *k* is a further stage; *l* shows the filament splitting in each pronucleus, but each first segments transversely into two; the pronuclei are closely applied to each other in a bilateral way, as seen by the position of the polar asters, which now appear (*m*). The loops finally arrange themselves in the equator, so as to show in polar view as in *n*; two of these loops were furnished by the male and two by the female. A side-view of this stage is shown in *o*, where the filaments have split in the middle, but not yet at the ends and the centre. In *p* the V-shaped loops have diverged towards the poles quite a ways; the central apices, however, move faster towards the poles than the outer limbs. *q* shows the microsomata somewhat irregularly segregated at the base of a figure formed by the polar aster and spindle of conducting fibre, and at the apex of the spindle of connecting fibrils, which is now constructing the cell-plate as in *s*. This seems to show that the *connecting fibres* and the *conducting fibres* belong to distinct systems, which is more clearly shown in *r*, where the karyosomata are placed at the cross-points of the meshes formed by the interlacing of the two systems. In the construction of the daughter-nucleus the microsomata pass by segmentation into a knäuel like that seen in *j* and *k*, and only when the equatorial plate is again formed for subsequent division do we get the four loops once more established, as is seen respectively at the left and right of *s*. Van Beneden, however, ignores the evidence of his own figures, and states that the four loops remain distinct throughout. (See text for further discussion.)

PLATE VIII.

FIG. 125, *a–e*. From the segmenting egg of the *Axolotl*—Bellonci, Arch. Italiennes de Biol., vi.—Shows how the knäuel reticulum is formed from the loops. The loops in this case are hook-shaped, or almost straight rods, the end of the segment which first reaches the pole swells out and the chromatin breaks up into microsomata, the whole segment is thus transformed into a vesicle containing peripheral microsomata. These vesicles fuse as in *c*, *d*, *e*, and the microsomata become arranged in rows, which thus form a reticulating filament.

FIG. 126, *a–k*. Fertilization of ovum of *Arion empiricorum*—Platner, A. m. A., xxvii.—In *a* we see the polar globule (*pg*) and the spermatozoon (*sp*), whose head and neck have penetrated into the egg, but left the tail free. The head consists of a hyaline material holding two karyosomata. As usual astral rays surround it. The germinal vesicle contains many karyosomata, each with a hyaline envelope. The head of the spermatozoon at last becomes included in the germinal vesicle. In *b* we see the karyosomata have broken up into many microsomata arranged at the periphery of each hyaline vesicle, they fuse, so that for the most part, as in *c*, each shall

contain two microsomata at opposite sides. But the hyaline vesicles themselves fuse (or divide?) as indicated by the dumb-bell forms in *b*. The hyaline mass of the male pronucleus divides, so each half has a karyosoma, and the latter passes through the same stages of segmentation and fusion as the female karyosoma, except that each vesicle has finally four microsomata instead of two (*c*, *d*, *e sp*). [Only the germinal vesicle or its contents are shown in all figures except *a*.] On the side of the germinal vesicle towards the centre of the egg there arises an aster (*c*), and some of the hyaline vesicles become club-shaped and send out stalks and put themselves into connection with it, the membrane of the germinal vesicle disappearing at this point. In *d* a second aster has arisen, also near the first, so that the two are not at first opposite each other, but become so more and more by swinging around into a right line, and as they do so the germinal vesicle sinks towards the interior of the egg; the remaining microsomata, like the first lot, now become connected with this aster, except that the male karyosomata are behindhand (*d*, *e*), but finally these also join. Meanwhile the microsomata become regularly disposed in an equatorial plate and grouped in fours, each pair of a four being united by a spindle-fibre to its own pole (*f*). Then each group of four microsomata fuse to form one karyosoma on each fibre (*g*), and again segmenting into four (*h*), they separate, leaving connecting fibrils between them. As the microsomata move polewards there is a stage, as usual, where they seem to fuse laterally (*j*). In *k* we see the spindle turned out of its position, leaving the two large polar asters *in situ*, but still possessing little ones of its own. Such is the history of the first segmentation after fertilization. By comparing it on the one side with Fig. 124, and on the other with Fig. 127, it is seen to form a connecting link.

FIG. 127, *a–f*. A case of conjugation with *Vorticella microstomum*—Engelmann, M. J., i.—When division or budding takes place the nucleus stretches into the bud and is segmented off. These buds are the microgonidia or males, and may suffer segmentation like sperm mother-cells before being set free. The mother from which they budded is the macrogonidium, and is itself soon fertilized by a microgonidium, which is the child of another macrogonidium. *c* shows the first step in this conjugation. The nucleus, both in the macro- and the micro-individual, segments up into bits, smaller and smaller, and the microgonidium being absorbed, its microsomata are added to the more numerous microsomata of the female. Then there is gradual fusion until the single nucleus is reconstituted. Before this happens there may be division and budding, as in *a* and *b*. An exactly similar series of phenomena is described for *Epistylis plicatilis*.

FIG. 128, *a–e*. Conjugation of *Paramœcium*—Enc. Brit., "Protozoa."—This illustrates "temporary conjugation." *a* is a normal individual; *b*, two united for sexual ends. The nucleus and paranucleus divide successively, the former into many, the latter into four bits, and then they fuse again, only partially completed in *e*, but now the old nucleus becomes the new paranucleus, and the former paranucleus takes on the functions of the nucleus. The individuals separate and continue asexual division. This is probably an incomplete account of what happens. There is much controversy about this ill-understood process, but we must assume that there is mutual interchange of microsomata between the two individuals in harmony with some observations, and thus bring this process into line with what we know happens in all other cases of fertilization. (See text for further discussion.)

FIG. 129. Fertilization of egg of *Bat*—Van Beneden and Julin, A. B., i.—The two pronuclei are seen each in a vesicle lying in a clear space in the vitellus and in proximity to each other.

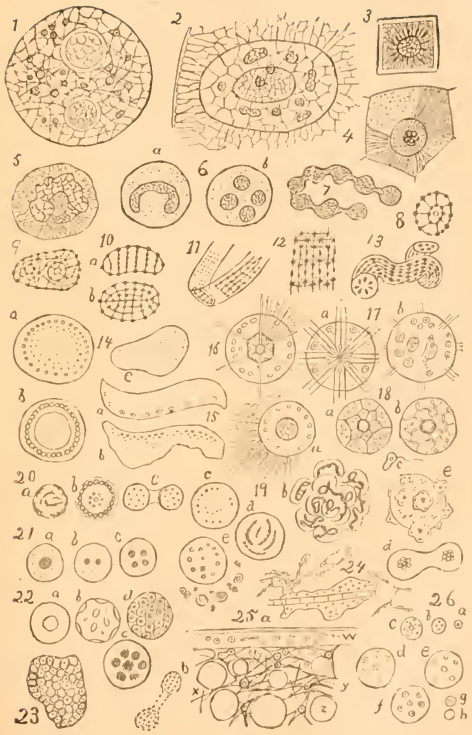
FIG. 130, *a–g*. Fertilization of ovum of *Sphærechinus brevispinosus*—Flemming, A. m. A., xx.—In *a* we see a large female pronucleus, and a smaller male pronucleus in the egg. In *b* each has been crowned by an aster. The male pronucleus now moves towards and fuses with the female pronucleus (*c*). The chromatin of the male pronucleus may split as in *d*, but soon all the chromatin of the fertilized nucleus is transformed into a segmented "skein (*e*)." At the same time polar asters appear, whose rays drive the segments to the equator (*f*), where they arrange themselves in a regular plate, split, and pass to the poles, there constituting the daughter-nuclei, one of which is shown at *g*, still crowned by its aster.

FIG. 131, *a–b*. "Genetic blending" of *Dallingeria Drysdali*—J. R. M. S., April, 1886.—We may suppose the form with one flagellum, large nucleus, and granular zone to be female; then the form with three flagella and small nucleus is male. Both nuclei and bodies fuse to one individual, and then the nucleus is dissolved, and the cell is encysted, finally to burst, as myriads of spores, scarce visible under fifteen thousand diameters magnification.

FIG. 132, *a–d*. Fertilization phenomena in *Orchis latifolia*—Strasburger, Befruchtungs Vorgang bei den Phanerogamen, Jena, 1884; see also Jen. Zeits., xi.—Two sorts of nuclei, "germinative" and "vegetative," are found in the pollen-grain and tube, and these may multiply by karyokinesis. The former alone act as male pronuclei, and where there is more than one, the first one to make its way to the egg does the fertilizing; the others then are passive. The nucleus of the embryo-sac dividing sends each daughter-nucleus to its own pole, and there each undergoes division twice, producing four nuclei at each end of the sac. Then one of these from each end meet and conjugate in the centre (*z*) to form the mother-cell of the endosperm. Two of the remaining ones at the upper end (where the pollen tube enters) form the "synergids" (*s*) supposed to function in secreting a fluid attractive to the pollen-tube; the fourth becomes the ovum or female pronucleus (*y*). The three nuclei at the other end (*z'*) are the antipodal cells. In *a* the male pronucleus has entered the ovum. In *b* the two have fused, but the nucleoli are still separate. In *c* the nucleoli are one; and in *d* the first segmentation spindle of the embryo is formed.

FIG. 133. A segmentation spindle from the egg of *Aulostomum gulo*—Nussbaum, A. m. A, xxvi.—To show the direct continuity of spindle-fibres with the yelk reticulum.

PLATE I.


1
2
3
4
5
a
6
b
7
8
9
10
a
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11
12
13
a
14
c
15
a
b
16
a
17
b
18
a
b
19
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c
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e
20
a
b
c
21
a
b
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22
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b
c
d
23
b
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26
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y
z

PLATE II.

PLATE III.

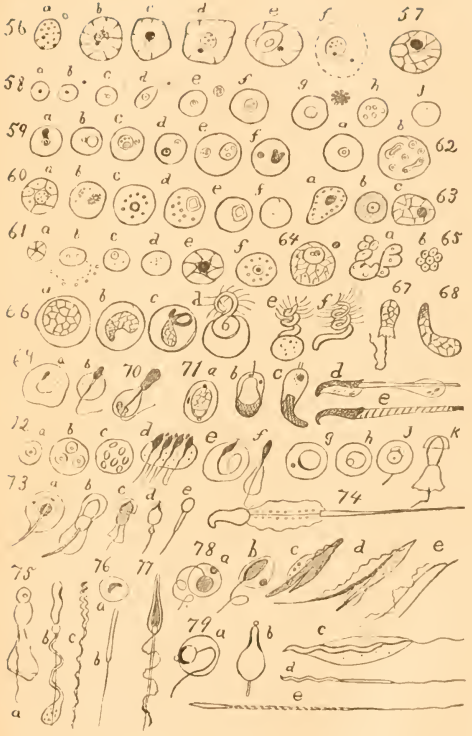

PLATE IV.

80 a b c d e
81 a b c d e f
82 a b c d e z
83 a b c d e
84 a b c d e f g
85 a b c d e
86 a b c d e f g h
87 a b
88 a b c d
89 a b c d e f g
90 a b c
91 a b c d e f g h
92 a b c d e
93 a b c d
J

PLATE V.

94 a
b
95 a
b
c
d
96 a
b
97 a
b
c
d
97½ a
b
108
98 a
b
c
d
e
f
g
99 a
b
c
100 a
b
c
d
101 a
b
c
d
e
107
102 a
b
c
110
103 a
b
c
d
e
f
g
h
j
k
l
m
n
o
i
104 a
b
c
105 a
b
c
d
e
f
109
g
h
j
106 a
b
c
d

PLATE VI.

PLATE VII.

PLATE VIII.

124
S
125
a
b
c
d
126
a
b
c
ε
d
f
g
h
j
k
ε
127
a
b
c
d
ε
f
128
b
c
d
a
ε
d
129
130
a
b
c
f
g
ε
131
a
b
132
a
b
c
d
133